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**CONTENTS**

**THE RÔLE OF ENVIRONMENT IN THE  
LIFE OF BIRDS**

**S. CHARLES KENDEIGH**

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# ECOLOGICAL MONOGRAPHS

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## THE RÔLE OF ENVIRONMENT IN THE LIFE OF BIRDS

By

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Cleveland, Ohio*

CONTRIBUTION NO. 28 FROM THE BALDWIN BIRD RESEARCH LABORATORY, GATES MILLS, OHIO, AND  
NO. 449 FROM THE ZOOLOGICAL LABORATORY OF THE UNIVERSITY OF ILLINOIS, URBANA, ILLINOIS



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# THE RÔLE OF ENVIRONMENT IN THE LIFE OF BIRDS

## I. INTRODUCTION

Ecology has been defined as the study of animal and plant communities. This is permissible because the aim of ecological research is to study the natural phenomena of biotic relations—and no organism exists alone. The community is the unit of biotic interaction and expresses not only the relation between organisms but also that between organisms and their environment.

The study of biotic communities may be approached from two directions. Research may be directed towards analyzing the composition, responses, and relations of the community as a whole. Such studies are necessary to orientate the entire field and to determine the major points of importance. On the other hand the component members of the community may be separately studied in more detail. The information thus obtained may be correlated for an understanding of the community. The present paper approaches the study from this second point of view.

The community concerned is the *Quercus-Fagus* Formation (deciduous forest) and the particular component members emphasized are the passerine birds. As the eastern house wren, *Troglodytes a. aedon* Vieillot,<sup>1</sup> is the species selected to represent the group, most of the discussion applies directly to it. The species is typical in its behavior and responses of a large portion of the avifauna of this community, particularly the portion that is regularly migratory in habit, but is less typical of that group which remains permanently resident throughout the year. Likewise, it is not certain how far the species represents forms of lower phylogenetic rank than the Passeriformes. Particular emphasis will be put on the rôle of environmental factors in determining the behavior, distribution, migration, and abundance of the species, since these factors are of great importance in determining the status of any species in a biotic community.

The writer wishes at this point to express his appreciation of the advice and suggestions given him from time to time during the course of this work by Dr. Victor E. Shelford of the University of Illinois. The working out of the climographs and the application of the experimental data to the theoretical problems concerned was performed largely in his laboratory. To Dr. S.

<sup>1</sup> Recent investigations indicate that the house wren in Ohio may belong to a new subspecies (Oberholser, Ohio Jour. Sci. **36**(2), 1934, 86-96). If this is accepted, the discussion in the following pages and the diagram (Fig. 1) must be considered to include both this new subspecies and the eastern house wren. There is no present evidence to warrant belief that differences exist between these two subspecies in fundamental physiological or ecological reactions. The present study, therefore, is of that portion of the house wren population, regardless of subspecies, included within the distributional boundaries indicated. Scientific names of species included in this paper are taken from *Checklist of North American Birds*, fourth edition, 1931.

Prentiss Baldwin, he wishes to acknowledge personal encouragement and co-operation in many ways and the privilege of drawing freely upon experimental and other data accumulated during the course of years at the Baldwin Bird Research Laboratory. The following assistants have aided materially in performing the experimental work: Mr. James Stevenson, Mr. T. C. Kramer, Mr. Carl Johnson, and Mr. H. E. Wallin. Considerable data on distribution of the eastern house wren were obtained through the courtesy of Dr. W. B. Bell and Dr. H. C. Oberholser of the U. S. Biological Survey, Washington, D. C. The manuscript was given critical readings by Dr. S. Prentiss Baldwin, Dr. Victor E. Shelford, and Dr. Frederic E. Clements.

## II. DISTRIBUTION, MIGRATION, AND ABUNDANCE OF THE EASTERN HOUSE WREN

### DISTRIBUTION

An exact knowledge of the distribution and local abundance of the eastern house wren had to be determined before the breeding and winter ranges could be characterized climatically. Hundreds of breeding records with numerous notes of local abundance were obtained from the files of the Biological Survey at Washington, D. C. In addition to these, resource was had to numerous state and faunal lists and to some correspondence. All records were plotted on a large scale base map of North America. Boundaries were then drawn to indicate limits of distribution and also comparative abundance (Fig. 1). The winter range of the species was determined from data compiled from literature. The Christmas Census reports in *Bird-Lore* were an important source of information. The records indicate that though individuals may occasionally winter as far north as New Jersey, the species is more common further to the south and is abundant in Florida.

For several reasons it is advisable to confine the discussion to the eastern form of the house wren.<sup>1</sup> The western house wren, *Troglodytes aedon parkmani* Audubon, extends directly westward from Illinois and southern Missouri to southern British Columbia, central Alberta, central Saskatchewan, southern Manitoba, and northern Wisconsin, south to lower California, southern Arizona, and central western Texas. It winters from California and Texas southward into Mexico, and occasionally in northern and central Florida.

In order to compare the distribution of the eastern house wren with, and to determine its position in the deciduous forest biome, the need arose for a map of the ecological communities occurring in the eastern part of North America. As none with sufficient detail was available, it was necessary to construct an original one. The first step in the construction of a map showing

<sup>1</sup> See footnote, page 301.

biotic, or true ecological communities, consists in showing the climax vegetation, and that is what is presented in Figure 2. Information for constructing this map was obtained from original notes, review of literature, and correspondence. For the last ten years, the author has been accustomed to make notes on the ecological nature and composition of the vegetation wherever he has been, and as he has made frequent trips through a large part of this



FIG. 1. Diagram of breeding and wintering ranges of the eastern house wren. The localities indicated are those from which climatic data were obtained.\*

region, these notes furnished a background in the making of the map. These trips have extended to Charleston, South Carolina, through much of Kentucky and Tennessee; south to New Orleans, Louisiana; west to eastern Nebraska, Illinois, Wisconsin, Michigan; from Toronto and Ottawa to Quebec and then south in Canada; New England north to southern Maine; Adirondack Mountains, New York; northern Pennsylvania; all of Ohio;

\* See footnote on page 301.



south through the Appalachian Mountains, and intermediate areas. In addition, several years residence in northern Ohio gives the author some intimate acquaintance with that region, and two years in central Illinois and one year in Lincoln, Nebraska, allowed him to study the transition of the deciduous forest into prairie.

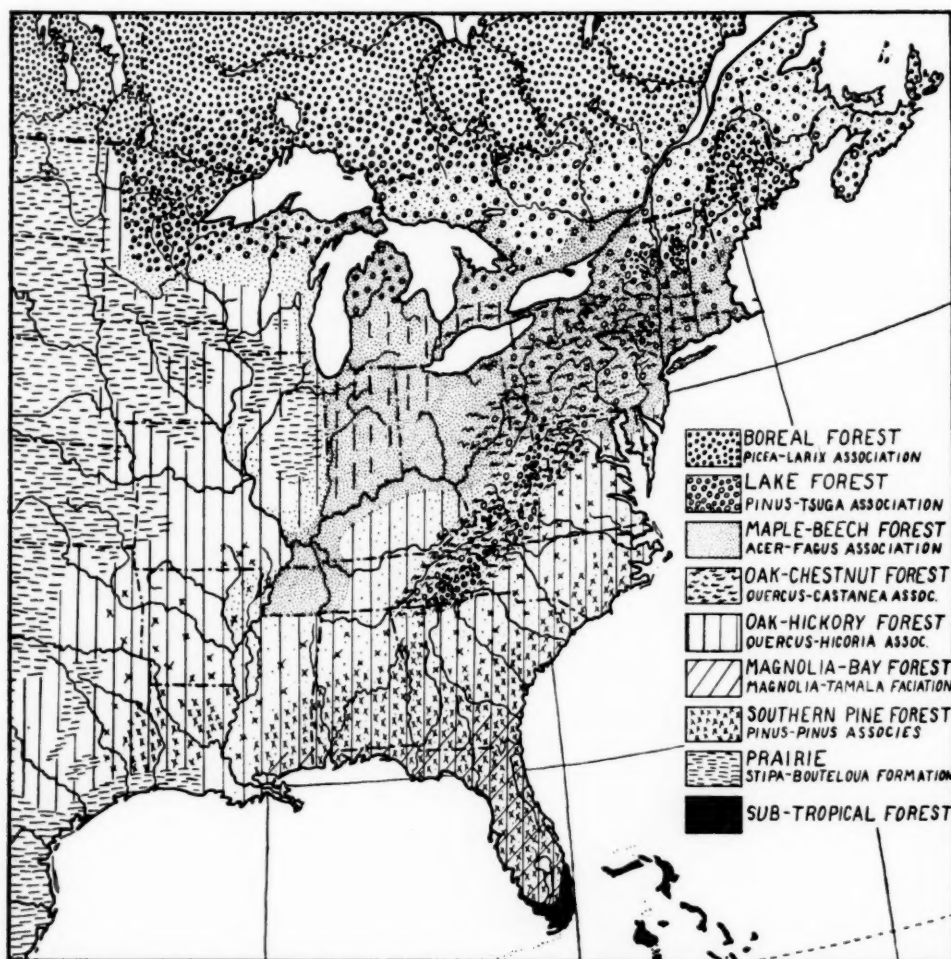


FIG. 2. Diagram of major ecological communities in eastern North America. Each community is shown by a distinctive symbol, and the density of the symbols indicates the relative development of that community in that region. The overlapping of symbols indicates the occurrence of two or more communities in the same region, representing mixtures, transition areas, faciations, or subclimaxes.

A rather thorough review of the literature was made by which the most important references have been covered. *The Naturalist's Guide to the Americas* (Shelford 1926) proved a particularly fertile source of information. Considerable use was made also of the vegetation map of Shantz and Zon (1924) and the text-book of Weaver and Clements (1929). The terminology used is that presented in Weaver and Clements' text-book.

Valuable notes and constructive criticisms were also obtained from Dr. V. E. Shelford, Mr. A. S. Hyde, Mr. C. C. Goff, Miss Hilda A. Stein, and Miss Lucile Rice at the University of Illinois; Dr. F. E. Clements of the Carnegie Institution; Mr. H. C. Jones and Dr. Lynds Jones at Oberlin College; Dr. J. E. Weaver of the University of Nebraska; Dr. C. D. Howe, Dean of Forestry, University of Toronto; Prof. Frère Marie-Victorin, Université de Montreal; Mr. M. L. Grant of the University of Minnesota; and Mr. H. V. Truman of the University of Wisconsin.

The diagram (Fig. 2) does *not* represent all the different types of vegetation as they exist at the present time. This is because a large percentage of the area is in seral or developmental stages which, except in a few instances, are not mapped. Climax communities (in the ecological sense) better express the influence of climate upon vegetation and the division of the country into biotic units. For further discussion and explanation of these communities, the reader is referred to Weaver and Clements (1929) and Shelford (1926). The different communities are not sharply separated, geographically, from each other. Boundary lines for the different communities have been purposely omitted. The overlapping of symbols is intended to give some idea of the way and the extent to which the different communities themselves do actually overlap.

Comparison of the distributional diagram for the eastern house wren (Fig. 1) with that for the plant communities (Fig. 2) brings out an interesting and significant correlation. The breeding area of the eastern house wren falls largely within the *Acer-Fagus* (maple-beech) Association. The outermost limits in the distribution of the bird fall largely in the ecotone or transitional areas around this association. Westward, the bird's place is taken in the *Quercus-Hicoria* (oak-hickory) community and prairie areas by the western house wren (Butler 1891). On the south, the breeding range of the eastern house wren overlaps the *Quercus-Castanea* (oak-chestnut) Association and a small portion of the *Quercus-Hicoria* Association, but the *Acer-Fagus* Association occurs also in local communities as an overlap into these same regions. The eastern house wren may, therefore, be considered a characteristic member of the *Acer-Fagus* Association.

The eastern house wren is not confined to nor characteristic of the climax community itself but occurs throughout the seral stages wherever there are suitable nesting sites. It is a member of the aestival, serotinal, and early autumnal aspects. At times, as in secondary communities after fire, it might be classed as a seasonal predominant, but ordinarily it is only a part of an animal society or societies.

The fact that the house wren is common now about dwellings and human habitations means not that the house wren has changed its habitat relations, but that its native environment has been expanded through the efforts of man.

Shrubs, insect food, and nesting sites around human dwellings are ecologically equivalent to secondary communities which develop on burned areas or where physiographic disturbances have occurred in the native forest.

The bird is not a permanent resident in the association but spends the winter in the South Atlantic and Gulf States. Here it is found in the southeastern part of the area covered by the *Quercus-Hicoria Association*.

#### MIGRATION

The first house wrens arrive in northern Ohio about April 25, but do not become common until about May 1. This median date first seen, as determined by Dr. Lynds Jones for the Oberlin region, is from records covering twenty-four years. Oberlin is almost directly fifty miles west from the Baldwin Bird Research Laboratory. The earliest record of arrival is April 7, 1918. The male arrives a week or more before the female and begins the construction of the nest almost at once. Eggs are usually being laid by the third week in May, and young birds are being cared for by the second week in June.

The exact time that house wrens begin to leave for the south in the autumn is not known. Young birds from the first nesting of the season are placed largely on their own independent resources by July, and some wandering takes place then, although not to any great distance. Frequently, small groups may be found in favorable places day after day during July and August. Some of these groups, of which daily account had been kept for several weeks, have disappeared with the coming of the first cool nights in the latter part of August. Migration probably begins at that time. The median last date for the occurrence of house wrens in the Oberlin region is October 1, though the latest record is October 15, 1906.

#### ABUNDANCE

Local differences in the abundance of the house wren have already been indicated (Fig. 1). Around the periphery of the species' breeding range, particularly in the north and south, the bird becomes uncommon or rare before it disappears altogether. This decrease in abundance is probably correlated with the variation of one or more environmental factors towards the limit of tolerance of the bird (Shelford 1913, p. 303). One purpose of this study is to analyze the geographic variation in environmental factors in order to determine, if possible, the controlling factors in the local abundance of birds.

A fact well known to field students of animals is that not only is there geographic variation in the abundance of birds, but that in any one locality the abundance of a species may fluctuate from year to year (Elton 1924, Huntington 1931). At the Baldwin Bird Research Laboratory, a record is



available of the number of house wrens breeding on an area of fifteen acres over a period of thirteen years (Table 1). As sufficient nesting boxes were provided at all times, it is believed that the fluctuation in numbers from year to year is a natural one and not caused by human agency or interference.

TABLE 1—*Abundance and reproduction of house wrens on fifteen acres at the Baldwin Bird Research Laboratory, Gates Mills, Ohio.*

Year	Number of pairs	Total number of broods	Number of broods per female	Relative abundance	Relative amount of reproduction	Relative survival over following winter
1921	9	16	1.8	Average	Above average	Below average
1922	9	15	1.7	Average	Above average	Average
1923	11	14	1.3	Above average	Average (—)	Average (—)
1924	9	13	1.4	Average	Below average	Above average
1925	9	14	1.6	Average	Average (+)	Below average
1926	6	7	1.2	Below average	Below average	Average
1927	7	11	1.6	Below average	Average (—)	Average (—)
1928	8	13	1.6	Below average	Average	Above average
1929	11	17	1.5	Above average	Above average	Average
1930	11	17	1.5	Above average	Above average	Below average
1931	9	15	1.7	Average	Above average	Average
1932	10	13	1.3	Above average	Below average	Above average
1933	14	17	1.2	Above average	Average	.....
Ave.	9.5	14.0	1.5			

In addition to these records of nestings on the fifteen acres immediately surrounding the laboratory, frequent visits have been made during every breeding season since 1926 to every house wren box within a radius of about a mile. At these boxes, an attempt has been made to capture and band all the adults and young and to carry on other studies. As the number of available nesting boxes has varied from 98 in 1926 to a maximum of 280 in 1930, an analysis of fluctuations in a large population has been possible. The number of adult birds per available box has varied during the last eight years as follows: 1926—0.73, 1927—0.97, 1928—1.02, 1929—1.20, 1930—1.15, 1931—0.83, 1932—1.11, and 1933—1.44. A comparison of these figures with those given in Table 1 for the "Number of pairs" shows a very close agreement in yearly fluctuations of the breeding population in this region.

These records probably indicate similar fluctuations in abundance of the bird all over the breeding area. This is checked for the year 1926, when there was a period of marked reduction in the population, amounting to 36.8% from the average for the thirteen years. A number of reports from other parts of Ohio and as far east as Washington, D. C., indicate that this condition prevailed all through the east. In some localities there was a decrease of as much as 75% or 100% from the preceding years. Likewise, Stoner (1932) found this species more abundant in the Oneida Lake region of New York in 1929 than in 1928, and this agrees well with our data. There

is some assurance, therefore, that the fluctuation in number of eastern house wrens on this unit area is at least a criterion of the major fluctuations throughout the area in which the subspecies breeds.

In estimating the total number of broods per season and the number of broods per female, care was taken to include all those in which a full set of eggs was laid, regardless of the outcome of these eggs. The computations were made in this way as it was believed that the more significant correlations between reproductive capacity and climatic factors could thereby be brought out. The relation between the successful or unsuccessful outcome of nests and environmental factors is not considered in this paper.

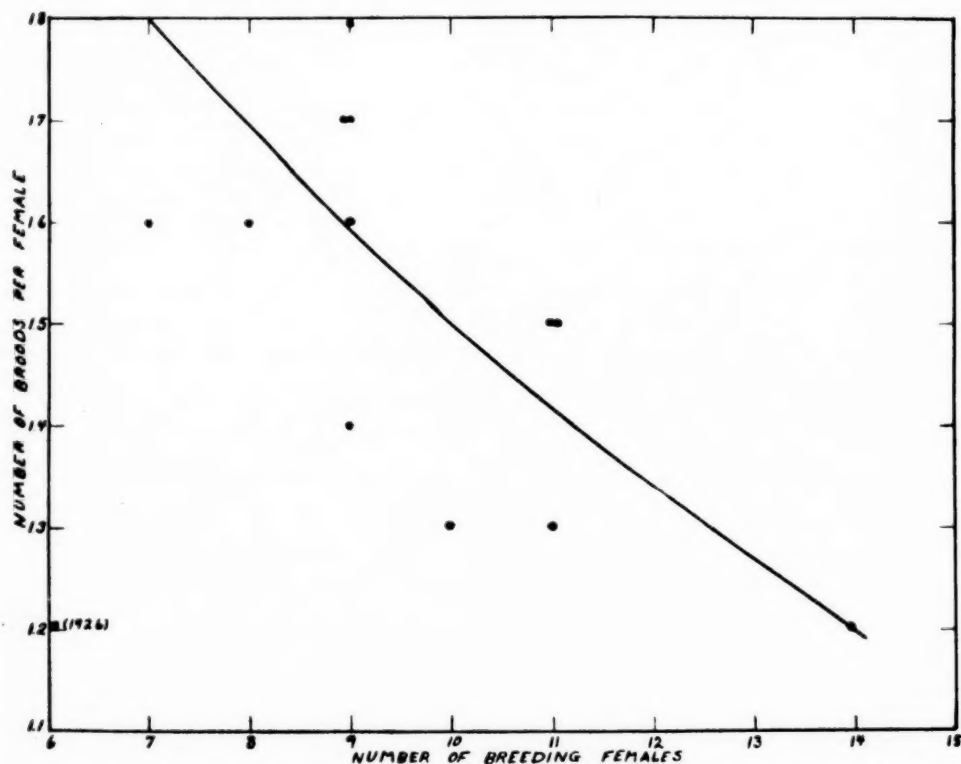


FIG. 3. Relation between number of broods per female and number of breeding females present on a unit area during successive years.

There appear to be three main factors involved in determining the relative abundance of birds from year to year. These are the number of birds breeding, the amount and success of reproduction, and the survival over winter. The number of birds breeding is both a cause and a result, a cause of abundance for the following year and the result or survival from the previous year. The relative amount of reproduction is stated in general terms in Table 1, giving about equal value to total number of broods and number of broods per female. The total number of broods from season to season,

but not the relative amount of reproduction, tends to vary roughly in the same manner as does the number of pairs of breeding birds. It is of particular interest, however, that the number of broods per female per season tends to vary inversely with the total population (Fig. 3). When the total population is reduced in size, the average of broods per female is greater than when the population is large. This compensating reproductive resiliency may not become effective the same year as a major calamity, as evidenced by the exception to this general correlation of the year 1926. An unusually large reduction in house wrens occurred in the preceding winter and spring of that year. This relationship complicates some of the correlations attempted in the following pages between amount of reproduction and climate.

To determine the survival over winter (Table 1), the abundance of the bird one summer as compared to the next must be considered, as well as the amount of reproduction. In 1921, the number of birds was average and reproduction considerably above average. From this, one would expect an increase in numbers nesting in 1922, if the survival over winter were average. Instead, the number remained the same. Probably, therefore, a large number died between the end of one breeding season and the beginning of the next. In this way, it was found that survival over winter was either average or above average in every year except 1921, 1925, and 1930. This is particularly beyond question for 1925, since that year the number breeding was average, the reproduction above average, yet the number present in 1926 considerably below normal.

In order to present some estimation as to the amount of mortality of house wrens involved in a winter with an average amount of survival to compare with winters when the survival is above or below normal, the following figures are offered. The average length of life of house wrens after once reaching sexual maturity is apparently not over two years. On the average, half or 50% of these older birds die every year. A female averages 1.5 sets of eggs per year, or 9 eggs. Thus in a two-year life span, 18 eggs will be laid. However, not all these eggs hatch into birds that survive to leave the nest. Of 133 nests of this species recorded during the years 1921 to 1930, only 68% were successful in rearing young. Out of 18 eggs, therefore, 68%, or 12, represent the number of young birds which each pair of adults will raise during the course of a lifetime. If the house wren population is to remain constant, only 2 out of these 12 birds, or 17% will live to reproduce and replace the adults. The mortality rate over winter among young birds averages, therefore, approximately 83%.

### III. TEMPERATURE

Though temperature has long been regarded as a controlling factor in the distribution and migration of animals and plants, greater importance formerly



was attributed to its rôle than is now by some scientists. With either plants or animals, various environmental factors as water, heat, evaporation, light, food, soil, biotic relations, etc., are important, and any one may at times be limiting. It is desirable to analyze the possible controlling rôle of each factor or combination of factors.

In determining the effect produced by any ecological factor, as temperature, upon such organisms as birds, three points need to be taken into consideration: (1) that the physiological and structural characteristics of the individuals and species are fundamental and condition all other responses; (2) that the behavior of the species is adjusted to make the most of these inherent characteristics and avoid circumstances that are detrimental; and (3) that the final ecological distribution, abundance, and relations of a species are the result and expression of the interplay of environmental conditions, behavior responses, and structural and physiological characteristics.

The structural characteristics of birds need not be considered in this connection except as they affect the physiology of bird temperature. It is only necessary now to point out the more significant phases in the physiology of bird temperature for an understanding of the rôle which temperature control plays in regulating the behavior and occurrence of the species. In another paper (Baldwin and Kendeigh 1932) the physiology of the temperature of adult birds, nestlings, and eggs have been discussed at some length, and further details as to the experiments and data, here summarized, may be sought there.

#### PHYSIOLOGY OF THE TEMPERATURE OF BIRDS

The standard temperature of adult eastern house wrens, at complete rest and without food in the alimentary tract, is, for the male, 104.4°F. (40.2°C.) and, for the female, 105.0°F. (40.6°C.). These values are fairly constant under various conditions, but may be lowered at night when the bird is inactive and without food for several hours. Variations in body temperature occur normally in passerine birds between the limits of 102.0°F. (38.9°C.) and 112.3°F. (44.6°C.) under natural conditions. Emotional excitement, muscular activity, extremely high air temperature, and the digestion of food cause a rise in body temperature, while starvation and extremely low air temperature produce a decrease. The decrease caused by starvation lowers the body temperature several degrees below normal. Seven individuals of three species (eastern house wren; eastern chipping sparrow, *Spizella p. passerina* Bechstein; English sparrow, *Passer d. domesticus* (Linnaeus), died when their body temperature had dropped to 91.1°F. (32.8°C.). Death in these birds was caused primarily by starvation and not solely by reduced body temperature. The body temperature of several house wrens, when not in a starved condition, has been lowered experimentally to much below this level without death resulting. An abundant and readily accessible supply of

food is therefore necessary for maintaining the normal temperature regulation and functioning of the body.

Fluctuations of air temperature that are not extreme and that are within the range to which the house wren and other passerine species are normally accustomed do not cause, under controlled experimental conditions, any marked changes in body temperature. Birds have a good temperature-regulating mechanism in feathers, air-sacs, and control of heat production. Under natural conditions a slight correlation exists between variations in average bird and air temperatures from day to day; but the variation in the average bird temperature may amount to only a few tenths of one degree while the average air temperature may vary 20°F. (11.1°C.) or more. Even this slight correlation may not be a direct one but dependent upon variations produced in the amount of activity of the bird from day to day.

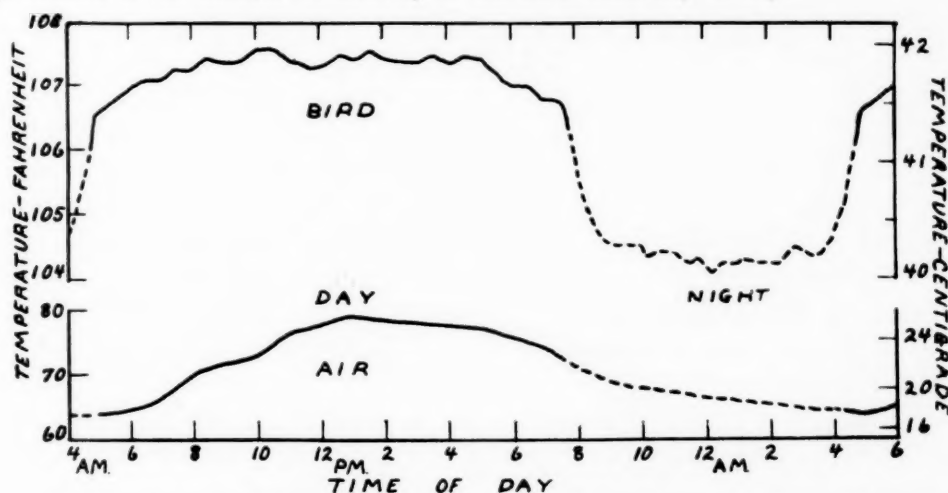


FIG. 4. Average daily rhythm in body temperature of passerine birds (8 species, 12 individuals, 75 days) correlated with air temperature, and showing the effect of activity during the day (full line), as against the quiet of night (broken line).

A body temperature of 116°F. (46.7°C.) is fatal to some passerine birds, although a body temperature of 112°F. (44.4°C.) is frequently attained under perfectly normal natural conditions without fatal results. Under certain experimental conditions, the body temperature of a house wren has been lowered to below 75°F. (23.9°C.), yet the bird recovered when it was placed for a short time in a warm incubator. A body temperature of 71°F. (21.7°C.) is, however, lethal. The body temperature of many birds of nine species has been lowered to below 95°F. (35.0°C.), or even 90°F. (32.2°C.), with complete recovery, provided these lowered body temperatures were not produced by starvation. Starving birds are difficult to revive because they have too little in the way of food reserves upon which to increase their metabolism. Recovery of birds that have not been starved is possible in a warm room because the food reserves in the body are not exhausted.

There is a decided and rather abrupt daily rhythm of body temperature in passerine birds (Fig. 4). The body temperature rises gradually during the morning from the beginning of the day's activities until the maximum is reached at midday and early afternoon. It then decreases in a fluctuating manner in the afternoon. When the bird settles on the nest for the night, its body temperature falls very rapidly for a short time. It then decreases gradually until the minimum is reached about midnight. From about 2:15 a.m. the bird's temperature tends to rise gradually until 3:30 or 4:00 a.m. There is then a rapid rise in the body temperature of the bird during the short period just before leaving the nest for the first time in the morning. This daily rhythm of body temperature is explained on the basis of variation in activity and metabolism during the day and night. The daily rhythm in body metabolism appears to be fully as definite and distinct as is the daily rhythm in body temperature, being considerably lower at night than during the day (Burekard, Dontcheff, and Kayser 1933).

The average daily maximum body temperature over a half-hour period has been found for eight species of passerine birds to be 108.7°F. (42.6°C.), although temporary rises in body temperature even up to 112.3°F. (44.6°C.) are common. The average daily minimum body temperature was found to be 103.4°F. (39.7°C.) although the body temperature may occasionally drop to 102.0°F. (38.9°C.). The minimum body temperature normally comes at night when the stimulating effect of exercise is lacking and the bird is without food. The maximum body temperature normally comes during the daylight hours.

Nestling birds and eggs of altricial species do not, at first, have a temperature-regulating mechanism of their own. They are poikilothermic. This is reflected also in their metabolic reactions to changes in air temperature (Ginglinger and Kayser 1929). They are able, however, to survive a lowering of their body temperature to a considerably lower degree than adults can endure. Although the first high body temperature that becomes lethal to the adults is also lethal to the nestlings and eggs, they are able to tolerate a higher air temperature. Temperature control in the house wren is established nine days after hatching. A study of temperature conditions in the nest shows that as long as the adult birds are able to carry on normal activities, the survival and development of the young progress independently of environmental conditions. There is no present evidence that temperature may play a critical limiting rôle in the distribution, migration, and abundance of birds through affecting the development of eggs or young (Kendeigh 1932).

#### RESISTANCE OF BIRDS TO LOW AND HIGH AIR TEMPERATURES

Experimental work indicates that extremely high temperature has a more direct and immediate effect upon the health of birds than does low temper-



ature. The upper margin of safety between the highest normal body temperature and the lethal body temperature is only about  $3.7^{\circ}\text{F}$ . ( $2.1^{\circ}\text{C}$ .). The maximum endurable body temperature may be reached in midsummer when the air temperature gets above  $95^{\circ}\text{F}$ . ( $35.0^{\circ}\text{C}$ .), if the bird becomes very active or excited. The maximum air temperature reached during the day appears to be most significant, therefore, in the effect of high air temperature on birds.

Adult house wrens, in extreme cases, have survived a lowering in their body temperature of  $30^{\circ}\text{F}$ . ( $16.7^{\circ}\text{C}$ .), so there is a wide margin of safety here. Provided they have plenty of food, adult birds have considerable resistance to a lowering of their body temperature even under conditions of extreme cold. In an experiment, an eastern house wren survived a temperature of  $8^{\circ}\text{F}$ . ( $-13.9^{\circ}\text{C}$ .) for four hours, although the species is probably never subjected to such a low temperature under natural conditions. Other species on which we have experimented have survived similar temperatures for short periods. Rowan (1925) tells how captive juncos, *Junco hyemalis connectens* Cones, survived severe winters in Manitoba with the thermometer registering a temperature as low as  $-52^{\circ}\text{F}$ . ( $-46.7^{\circ}\text{C}$ .). The birds became markedly lethargic, however, and were unable to gather necessary food for their continued existence. When placed in a warm room they soon recovered and showed no ill effects. Low temperature, in itself, is probably not often destructive to birds because of the remarkable regulating mechanism they have for maintaining the body temperature.

Birds lose weight over night because they are unable to obtain food. This is proved by an extensive study of bird weights at the Baldwin Bird Research Laboratory during the last eight years. It is at night that the birds must remain largely inactive, and that the lowest normal body temperature and body metabolism, as well as the lowest point in other physiological processes are reached (Fig. 4). The resistance of birds, therefore, cannot be maintained so long nor so effectively at night as during the day. At night the birds need all their ability for resisting low air temperature, because it is then that the lowest air temperatures during the twenty-four hour period are attained. The night air temperature and the duration of darkness appear, then, to be most significant factors involved in the effect of low temperature on birds.

*Experiments*—With these matters in mind, a series of experiments was devised to test the significant points in the temperature resistance of birds under various environmental conditions. The birds were confined in small cages which allowed a certain amount of freedom and movement. No food or water was given them and they were kept in darkness to simulate as far as possible the night period out-of-doors. The birds were then placed in different air temperatures and their survival time noted. They were looked at, on

the average, once every 2.7 hours, day and night. Their time of death was computed by taking the midpoint between the last time they were seen alive and the time they were found dead. The greatest possible error, then, in the determination of this time was half of 2.7 hours or 1.4 hours. After some experience had been gained, and after it was learned that the survival time was considerably shorter at a low air temperature than at a high one, they were looked at more frequently at these lower temperatures to determine the time of death with even greater accuracy.

A wide range of air temperature was obtained by the use of heated rooms, basement rooms, a refrigerator, and an incubator. For the lower temperatures of from 0° to 40°F. (-17.8° to +4.4°C.), a refrigerator was used. This had an adjustable thermostat so that the temperature could be set at the degree desired. Such temperatures could be maintained within  $\pm 2^\circ\text{F.}$  (1.1°C.). Seven holes were drilled in the sides of the refrigerator so that ample ventilation could be controlled and maintained. Not more than two to four birds were used at a time in the refrigerator. A basement room, with windows and doors closed, maintained a temperature between 60° and 70°F. (15.6° and 21.1°C.) constant within  $\pm 2^\circ\text{F.}$  (1.1°C.). Ordinary room temperatures between 70° and 80°F. (21.1° and 26.7°C.) were also used, although these temperatures could not be maintained so nearly constant. For the higher temperatures of from 90° to 105°F. (32.2° to 40.6°C.), a small incubator with thermostatic control was used which could be set at different temperatures and was accurate within  $\pm 1^\circ\text{F.}$  (0.6°C.). Tests indicated that there was ample ventilation in the incubator, and usually only one bird, and never more than two, were inserted at the same time.

Nearly all the experiments were made with English sparrows, *Passer d. domesticus* Linnaeus, since, as the preliminary work required the use of a large number of birds, it was not desirable to sacrifice any more of the native birds than were necessary. All birds were used directly after they were taken from the traps in which they were caught out-of-doors and in which they had been feeding. If any delay unavoidably occurred, the birds were not used. All birds, then, were taken directly after they had been feeding, and probably all had some food undergoing digestion in their stomachs. Their resistance against low temperature was, therefore, at the maximum at the beginning of the experiment.

A source of possible error was soon discovered. Birds trapped and started in the experiments in the morning did not have as long a resistance or survival time as did those started in the afternoon. In some instances with birds caught early in the morning, the survival time amounted to only one-third of that of birds caught in the afternoon. The reason for this is plain. The birds had been without food for several hours overnight and had not yet replenished their food reserves and thus increased their resistance in

preparation for the night to come. As a consequence, no bird that was caught before noon was used in experiments. After this there was no difference in the bird's survival time correlated with the time of day. All records, unless otherwise stated, were obtained during the summer months from the last of May until the first part of September.

*Survival time of English sparrows at different air temperatures*—In most of the work, care was taken to keep the temperature of the air constant during the experiments with the birds. Later work to determine the effect of a fluctuating temperature compared with a constant temperature indicated that there was no significant difference at medium degrees in the survival time of the birds (Table 2).

TABLE 2—*Effect of a fluctuating air temperature on survival time of English sparrows without food. Birds kept in darkness, humidity variable.*

Number of birds	Average air temperature		Fluctuation in temperature		Survival time: hours
	°F.	°C.	°F.	°C.	
4	14.1	— 9.9	16.0	9.0	11.4
8	13.4	—10.3	none	none	10.0
3	67.8	19.9	16.0	9.0	34.2
18	67.7	19.8	none	none	35.8
16	77.1	25.1	16.0	9.0	39.0
computed	77.0	25.0	none	none	40.3

The reason for this lack of difference is readily seen in Figure 5. Variations in survival time are almost exactly proportional to variations in the medium range of temperatures. These data (Table 2) have been incorporated, therefore, with those that follow.

Table 3 gives the survival time of English sparrows at different air temperatures, and also data on the loss in weight of the birds during this period. The data are organized and averaged for unit ranges in air temperature of usually 10°F. (5.6°C.) each; *i.e.*, all experiments in which birds were tested at air temperatures between 0° and 10°F. (-17.8° and -12.2°C.) are averaged together to give one figure. Likewise all the air temperatures within this range to which the birds were subjected are averaged to give one figure. The same procedure was followed in all instances except above 90°F. (32.2°C.) where the averages were made for each 5°F. (2.8°C.) temperature range, because of the greater significance of the variations in length of survival time.

TABLE 3—*Survival time of English sparrows during summer at different air temperatures. Birds were kept in darkness without food.*

Number of records	Average air temperature		Average relative humidity: percent.	Survival time: hours	Initial weight of birds: grams	Weight of birds at death: grams	Total percentage of initial weight lost	Percentage initial weight lost per hour
	°F.	°C.						
13	7.0	-13.9	.....	11.4	26.7	22.9	14.2	1.2
12	13.6	-10.2	.....	10.5	27.2	23.3	14.3	1.4
13	24.3	-4.3	.....	14.1	26.4	21.9	17.0	1.2
16	34.8	1.5	88.7	17.9	26.2	21.0	19.8	1.1
21	67.7	19.8	83.0	35.6	27.6	19.7	28.6	0.8
16	77.1	25.1	60.5	39.0	28.4	18.8	33.8	0.9
16	92.2	33.4	56.0	47.9	27.8	18.2	34.5	0.7
16	97.1	36.2	46.6	32.6	25.8	18.4	28.7	0.9
12	102.3	39.1	36.0	13.6	26.4	21.1	20.1	1.5

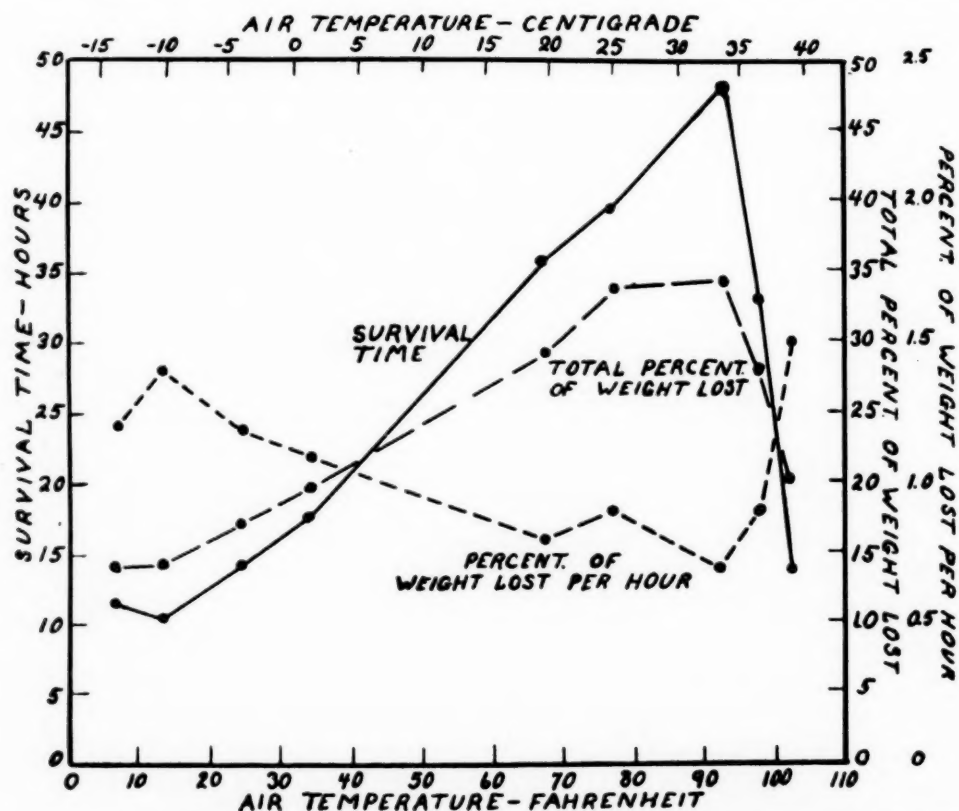


FIG. 5. Variation at different air temperatures of the survival time of English sparrows without food, of the total percentage in the initial body weight lost at time of death, and of the percentage in the initial body weight lost per hour.

The data presented in Table 3 and Figure 5 warrant careful consideration. Survival time between temperatures of 13.6°F. and 92.2°F. (-10.2°C. and +33.4°C.) is almost a direct linear function of the temperature. The



rise in the survival time at 7.0°F. (-13.9°C.) over what it is at 13.6°F. (-10.2°C.) probably indicates that the curve flattens out at these lower air temperatures. If the straight line between 92.2°F. and 13.6°F. (+33.4° and -10.2°C.) were extended to meet the base line of the chart corresponding with zero hours survival, it would do so at approximately -10.°F. (-23.3°C.). If the curve flattens out below 13.6°F. (-10.2°C.), as is indicated, it would not meet the zero base line until considerably lower. Survival time at air temperatures below 13.6°F. (-10.2°C.) is probably longer, therefore, than would be expected from the survival time of the bird at medium temperatures.

At an air temperature above 92.2°F. (33.4°C.) the survival time decreases at a very rapid rate. This decrease in survival time from 92.2°F. to 102.3°F. (33.4° to 39.1°C.) again follows a straight line, although at a sharper angle with the perpendicular, and if extended would meet the zero line of survival at about 106.0°F. (41.1°C.). The curve may, however, flatten out before doing so and not meet the zero survival line until a higher temperature.

The longest survival time comes at an average air temperature of 92.2°F. (33.4°C.). If the survival time of birds subjected to air temperatures between 90°F. and 95°F. (32.2° and 35.0°C.) are separated and averaged for each degree of temperature, the peak actually falls on 93.6°F. (34.2°C.), where the survival time for four birds averaged 53.8 hours. One bird survived 77 hours at 93.5°F. (34.2°C.), but the longest survival period of which there is record for any temperature is 84 hours at 98.0°F. (36.7°C.). Other birds placed at air temperatures above 95°F. (35.0°C.), however, lived a much shorter time so that the average for the higher range of temperatures is lowered. The turning point may be considered to come at 93°F. (33.9°C.), and it is at this temperature that birds can live the longest without food.

*Loss in body weight during survival period*—Some explanation of the decrease in weight during starvation may be made. There is a slight decrease in the weight of the whole bird at the very first caused by the elimination of undigested food contents from the stomach and intestines. Stevenson (1933) has shown that the last remnants of food in a filled stomach of song and field sparrows (*Melospiza melodia* (Wilson), *Spizella pusilla* (Wilson)) will be voided in 2.2 to 2.5 hours. The amount of this waste averages only about 10% dry weight of the food consumed, and so amounts to only a few insignificant milligrams. The great loss in the body weight of these birds during starvation (9.6 grams at 92.2°F. or 33.4°C.), cannot be accounted for by this alimentary elimination. Weighings of a few birds at intervals of a few hours through the survival period showed that the rate of weight loss was essentially uniform and constant throughout. In the experiments of Chossat (1843) with the starvation of pigeons, doves, chickens, and crows, the greatest relative loss in weight was found to occur during the first few hours through the elimination of faeces from the digestive tract. After the

first few hours the rate of loss in body weight slowed considerably, remaining fairly constant during the major part of the long starvation period. Chossat found that his birds lost 40% of their original weight before death, but he does not state specifically at what temperature they were kept. Nisimura (1930) found that doves died of hunger sooner in cold than in warm weather, their body weight falling by more than 40%. He also found that the loss in weight is most marked on the first day of starvation. Schimanski (1879) and Kuckein (1882) made intensive studies of starvation in the domestic fowl. A plot of the data that they give for the daily loss in weight of their starving birds shows clearly that this loss in weight was essentially uniform throughout the whole period. There was no marked excess loss during the first day from the elimination of faeces.

Voiding of excrement continues throughout the starvation period long after the stomach and intestines have been emptied. Under ordinary circumstances, excrement in passerine birds is voided about every half-hour. During starvation, this normal rate continues for a time, but later the interval between voidings increases. The excrement in these instances, does not contain hard food waste but has a decided watery constituency. Urinary wastes are excreted from the kidneys into the cloaca and are normally voided with the waste food from the intestines. This urinary waste is a semi-liquid substance and the voidings during starvation consist largely of this material. This would be expected because the urine is made up largely of the end products of metabolism, which must go on constantly as long as life persists. Much of the decrease in weight during starvation is attributable, therefore, to such voidings of excrement.

Water vapor is lost through the air-sacs and lungs and this may be considerable. Probably very little is lost on the body surface generally. Hari (1917) working with geese found that, at air temperatures from 80.6° to 82.4°F. (27.0° to 28.0°C.), 36% of the total heat lost was by evaporation of water, but at 60.8°F. (16.0°C.) only 20% was lost in this way. In recent work with the domestic fowl (Benedict, Landauer, and Fox 1932), it was found that at temperatures of 62.6° to 86.0°F. (17° to 30°C.) about 49% of the total heat lost is through the vaporization of water, primarily through the lungs. Kayser (1930) and Burckard, Dontcheff, and Kayser (1933) have measured moisture output in the pigeon and have found it to be greater at higher air temperatures. Water is, of course, also lost in the excrement.

In the experiments on the survival time of English sparrows without food, no water was offered the birds during the starvation period because it was desirable to keep the birds in the dark. In order to determine if this lack of drinking water would appreciably affect the survival time of birds without food, another experiment was tried of keeping two sets of birds without food but in the light and at a constant temperature of 67°F. (19.4°C.). No water

was allowed seven birds which served as controls, while small dishes of water were placed in the cages with nine experimental birds. The controls without water lived 26.7 hours while the experimentals with water lived only 23.6 hours. The experimental birds must certainly have been aware of the presence of the water, since they had jumped in and out of the dish and spattered water over the cage. Either the loss of water from the body did not induce a thirst craving in the birds, or, if it was consumed, it did not increase the length of the survival period. Though English sparrows do drink water under natural conditions, particularly during hot weather, many birds probably obtain most of the water that they require from the food which they consume. This is particularly true of insectivorous species.

In order to analyze more definitely the nature of the loss in weight of birds without food, another series of experiments was carried out. In the first experiment the object was merely to determine the total output of moisture in the respiration and faeces over a given period of two hours at a room temperature of approximately 72°F. (22.2°C.). All the birds used were English sparrows. The bird was placed in an oblong glass tube of ample size through which a continuous current of air was maintained by means of an aspirator. All connections were sealed with wax and careful control tests were made. On the floor of the glass tube a tray was placed for catching excrement voided by the bird. The bird was kept quiet and in the dark during the experiment by means of a black cloth thrown over the tube. The moisture was removed from the air before it entered the bird tube by first passing the air through two Erlenmeyer flasks containing calcium chloride. At the beginning of each experiment, after the bird was inserted into the tube, a preliminary circulation of a half an hour was made to free the air already in the tube of foreign moisture. Erlenmeyer flasks containing calcium chloride were inserted in the air outlet from the bird tube in order to collect all the moisture given off by the bird in respiration and in faeces. The amount of moisture given off by the bird was computed by the increase in the weight of the Erlenmeyer flasks at the end of the two hour period. To this was added the weight of moisture lost from the faeces when dried over a Bunsen burner. The results of this experiment are given in Table 4.

From Table 4, it is evident that the loss in moisture from the body makes up a large proportion (67.6%) of the bird's loss in weight when deprived of food, and that the loss in the dry faecal matter makes up only a relatively small proportion (9.1%). As starvation proceeds over several hours the loss due to dry faecal matter would become considerably less. The loss in weight unaccounted for (23.3%) is very probably the surplus weight of carbon-dioxide eliminated in the lungs over the weight of oxygen absorbed in the normal process of respiration, although this was not measured.

Knowing, then, that loss of water from the body accounts for a large

TABLE 4—Analysis of weight lost by English sparrows during a period of two hours without food.

Bird	Initial weight of bird: grams	Total loss in weight of bird: grams	Loss due to moisture given off		Weight of dried faeces		Loss in weight unaccounted for	
			Grams	Percentage of total loss	Grams	Percentage of total loss	Grams	Percentage of total loss
1	23.180	0.628	0.464	73.2	0.087	12.3	0.077	14.5
2	20.625	0.558	0.420	75.3	0.084	15.0	0.054	9.7
3	24.137	0.444	0.337	75.9	0.042	9.5	0.103	14.6
4	25.058	1.002	0.847	84.5	0.019	1.9	0.116	13.6
5	24.803	0.391	0.211	53.9	0.050	10.3	0.130	35.8
6	28.126	0.735	0.613	83.2	0.062	8.4	0.060	8.4
7	22.575	0.772	0.398	44.2	0.044	5.7	0.340	50.1
8	23.432	0.458	0.246	53.6	0.065	14.2	0.147	32.2
9	21.478	0.523	0.317	60.5	0.027	5.2	0.179	34.3
10	26.353	0.390	0.281	72.2	0.035	8.3	0.074	19.5
Ave.	23.977	0.590	0.413	67.6	0.052	9.1	0.125	23.3

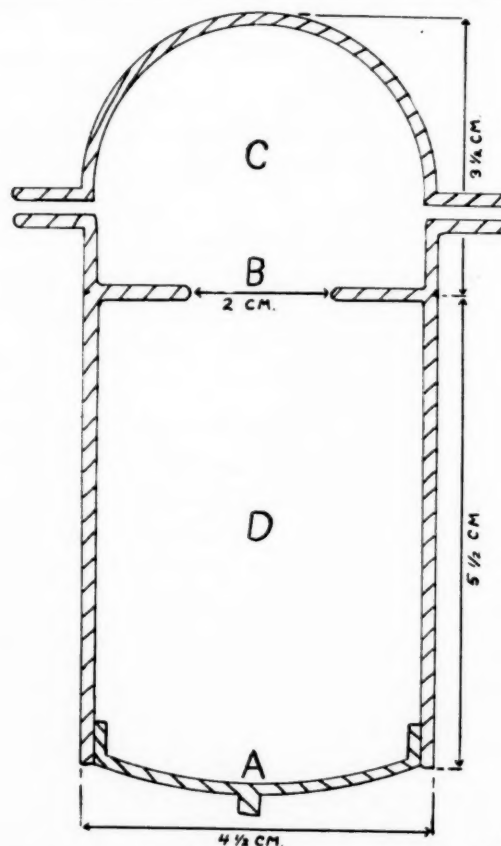


FIG. 6. Bird chamber used for determining the amount of moisture given off by English sparrows through the lungs. The birds were inserted into the chamber by removing the cap at A and pushing the head of the bird through the narrow opening at B. The head of the bird in final position was in compartment C, through which a current of air was maintained, while the rest of the body and the voided excrement were in compartment D, where little or no circulation of air occurred.



part of the loss in weight of birds during starvation, the next experiments were designed to discover what proportion of this loss in weight takes place through moisture given off by the lungs and how this moisture loss through the lungs varies in amount at different air temperatures. Moisture lost through the lungs should be, theoretically, directly involved in the temperature regulation of the body and should have considerable importance in determining the tolerance of birds to different air temperatures. A similar arrangement of apparatus as that just described was used in these experiments, except that a specially constructed bird chamber (Fig. 6) replaced the previous bird tube used. No food was given the bird for four hours before the experiment was begun; then the main feathers of the wing and tail were clipped short so that the bird could be inserted into the bird chamber; air, dried first by passing through calcium chloride, was forced through the bird chamber for half an hour before, finally, the calcium chloride flasks were connected to the outlet of the bird chamber to collect all moisture given off through the lungs of the bird during the experimental run of two hours. The bird was weighed just before inserting it into the chamber. Immediately after the experiment it was removed, killed with carbon disulphide, the feathers air dried for an hour, and weighed again. The experiment was always run with the bird in the dark. The chamber was of such small size as to be easily placed in a refrigerator or an incubator in order to obtain different temperatures. The results of the series of experiments are given in Table 5.

TABLE 5.—*Analysis of weight lost by English sparrows during two hours without food at different air temperatures.*

Air temperature		Initial weight of bird: grams	Total loss in weight of bird: grams	Moisture loss through lungs		Computed loss in weight due to voided excrement and excess carbon dioxide output over oxygen intake	
				Grams	Percentage of total loss	Grams	Percentage of total loss
°F.	°C.						
30	1.1	24.320	0.656	0.122	18.6	0.534	81.4
33	0.6	25.748	0.582	0.154	26.5	0.428	73.5
35	1.7	24.876	0.860	0.170	19.8	0.690	80.2
42	5.6	21.245	0.846	0.141	16.7	0.705	83.3
68	20.0	22.417	0.645	0.156	24.2	0.489	75.8
75	23.9	26.433	0.748	0.231	30.9	0.517	69.1
81	27.2	25.902	0.654	0.181	27.7	0.473	72.3
84	28.9	23.854	0.581	0.228	39.2	0.353	60.8
89	31.7	29.513	1.124	0.581	51.7	0.543	48.3
92	33.3	24.815	0.728	0.617	84.8	0.111	15.2
92.5	33.6	27.837	0.901	0.433	48.1	0.468	51.9
97	36.1	26.629	1.108	0.586	52.9	0.522	47.1
97	36.1	25.865	1.166	0.823	70.6	0.343	29.4

An examination of these data shows at once that the loss of moisture through the lungs makes up a larger proportion of the total loss in weight at high air temperatures than at low (Fig. 7). Below 70°F. (21.1°C.), there is little variation in the actual amount of moisture lost at different air temperatures, as moisture loss has practically reached a minimum. Between 70° and 85°F. (21.1° and 29.7°C.), the amount of moisture lost through the lungs begins to increase slowly with rise in air temperature, while above 85°F.

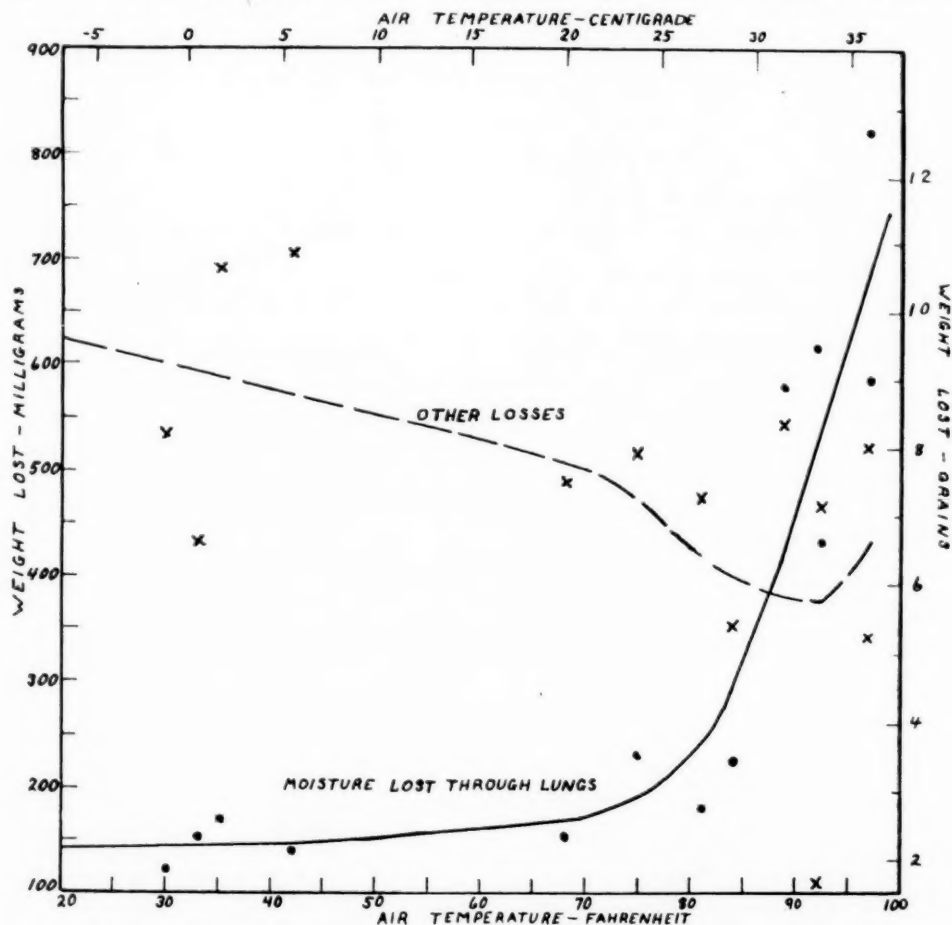


FIG. 7. Analysis of the loss in weight of English sparrows during two hours without food at different air temperatures. The actual loss in weight due to moisture given off through the lungs is separated from other losses due to excrement voided and to surplus carbon dioxide output over oxygen intake in the lungs.

(29.7°C.) further increases of temperature are joined with very rapid increases in moisture output. The evaporation of moisture through the lungs and air-sacs plays a very important rôle in temperature regulation at high air temperatures. The results obtained with the English sparrow agree well in general character with those obtained by Kayser (1930) with the pigeon.

Other losses in body weight occur through voided excrement from kid-

neys and excess output of carbon dioxide over the intake of oxygen in respiration, and these other losses furnish an index of the rate of metabolism. Figure 7 indicates that there is a marked increase in these losses as the air temperature decreases, which is in harmony with the results of other workers when explained on the basis of increased body metabolism (Groebbels 1927, Kayser 1930, Riddle, Christman and Benedict 1930). Benedict and Fox (1933) found that the rate of metabolism of the English sparrow during starvation at 86.4°F. (28°C.) was 656 calories per square meter of body surface per 24 hours and at 60.8°F. (16°C.) it was 914. Above 93°F. (33.9°C.) there is probably also an increase in these losses attributable to increased metabolism which in this case would be stimulated by rising body temperatures (Kayser 1927).

The percentage of the original weight of the bird lost each hour during the survival period furnishes, therefore, a rough index of the rate of body metabolism at air temperatures below 85° to 93°F. (29.7° to 33.9°C.), because, as has just been shown, it is primarily a measure of the rate at which metabolic wastes are eliminated and consequently of the rate at which the reserve food material in the body is utilized. Since the loss of moisture through the lungs is at or near a minimum and remains nearly constant it can be mostly disregarded. As shown in Figure 5 this rate of metabolism (loss in weight per hour) varies inversely with the length of the survival period, being the lowest at 93°F. (33.9°C.) and increasing as the air temperature decreases. At air temperatures above 85° to 93°F. (29.7° to 33.9°C.), the loss in weight per hour is less certainly an index of the rate of metabolism because it involves also an excessive loss of water through the air-sacs and lungs.

The total loss in body weight during the period of starvation is considerable (Table 3, Fig. 5). The greatest average loss in weight before death occurred is found in birds subjected to an average temperature of 92.2°F. (33.4°C.) where it amounts to 34.5% of the initial weight. This is a decrease in body weight from 27.8 to 18.2 grams. The very greatest loss in weight before death occurred in any of the birds experimented with is 41.7% at a temperature of 93.5°F. (34.2°C.), when the survival time was 77 hours. The lowest weight of a bird at death in these records is 13.7 grams. This bird lived 84 hours at 98.0°F. (36.7°C.), and had the unusually low body weight of 23.2 grams with which to start. These unusually large losses in weight are possible only at fairly high air temperatures, where the rate of metabolism has been reduced to a minimum, and where very little heat production is required to maintain the body temperature at the proper level.

At lower air temperatures, the total percentage loss in initial weight before death decreases until it is only slightly more than 14% at temperatures below 10°F. (-12.2°C.). The rate of heat loss from the body is augmented at lower air temperatures, and to compensate for this there must be an in-

crease in metabolism or heat production, if the normal body temperature is maintained. Death occurs sooner, therefore, at low air temperature than at high, because the readily accessible food reserves are soon depleted by the increased rate of metabolism and the less easily utilized reserves cannot be furnished the body fast enough or in sufficient quantity to maintain the metabolism. Death at lower air temperatures occurs, then, at a stage of food depletion when there is still sufficient food reserves left to maintain the bird for several hours at higher air temperatures. Body weight, therefore, is not decreased as much as it is at high temperatures when a minimum of metabolism is sufficient to sustain life in the birds for a long time. In starvation, the reserve stores of carbohydrates are probably drawn upon first, then the fats, and finally the proteins (Benedict and Riddle 1929). Recent work of Horst, Mendel, and Benedict (1930) in starvation experiments with the albino rat, wherein the metabolism was actually measured, confirms further the above explanation of differences in weight losses of birds at different temperatures. The work of Lusk (1919) is also of importance in understanding and corroborating the explanations of this and other experiments described in this paper.

*Individual differences in survival time*—There is considerable variation between individual English sparrows in the length of their survival without food (Table 6). This great variation between individuals in survival time is indicated also in the results of Chossat (1843), Schimanski (1879), and Kuckein (1882).

TABLE 6—*Individual variations in survival time of English sparrows in hours at different air temperatures. Birds were kept in darkness without food.*

Temperature range		Average survival time	Standard deviation	Longest survival time	Shortest survival time
°F.	°C.				
4.9 — 9.4	—15.1 — —12.6	11.4	± 2.5	16.5	6.5
11.0 — 19.5	—11.7 — — 6.9	10.5	± 3.2	15.0	4.5
20.9 — 29.7	— 6.2 — — 1.3	14.1	± 3.7	18.0	5.0
32.0 — 39.0	0.0 — 3.9	17.9	± 5.0	32.0	9.2
64.2 — 70.8	17.9 — 21.6	35.6	±10.3	61.8	22.0
74.6 — 80.1	23.7 — 26.7	39.0	± 8.7	54.8	25.2
90.1 — 94.3	32.3 — 34.6	47.9	±10.2	77.0	32.2
95.2 — 99.4	35.1 — 37.4	32.6	±17.0	84.0	6.0
100.0 — 104.8	37.8 — 40.4	13.6	± 8.5	27.2	5.0

The greatest standard deviation in survival time ( $\pm 17.0$  hours) comes in the range between 95.2° and 99.4°F. (35.1° and 37.4°C.). This is beyond the peak of the survival curve in Figure 5. The reason for this is that the high air temperature is not equally effective on all birds. Only those individuals which are unusually able in reducing their rate of metabolism can survive a longer time. This is illustrated by the fact that the longest survival



time (84 hours) of any individual in these experiments comes in this range. The majority of birds cannot, however, become adjusted sufficiently, so that some very short periods of survival are recorded. At low air temperatures, the standard deviation decreases, partly because the average survival time itself decreases, and partly because the effect of temperature is not so variable in different individual birds.

Differences in the initial body weight of individual birds have a considerable effect upon differences in survival time. The survival time of English sparrows in each range of air temperature, as given in Table 3, has been separated in Table 7 in order that approximately half the number of birds of greater weight may be compared with the other half which have a lighter weight.

TABLE 7—*Effect of differences in initial weight of English sparrows on their survival time at different air temperatures. Birds were kept in darkness without food.*

Number of birds	Average temperature		Survival time: hours	Initial weight: grams	Total percentage lost in weight	Percentage of initial weight lost per hour
	°F.	°C.				
7	7.1	—13.8	11.8	29.0	18.3	1.6
6	7.0	—13.9	10.8	25.8	14.7	1.4
5	16.5	— 8.6	11.9	29.2	15.1	1.3
5	12.6	—10.8	8.2	23.9	10.0	1.2
6	24.0	— 4.4	16.4	28.8	19.1	1.2
6	24.5	— 4.2	12.1	24.1	14.5	1.2
8	34.4	1.2	18.2	27.6	21.0	1.2
7	35.1	1.7	17.5	24.9	20.3	1.1
10	67.3	19.6	36.5	20.4	30.4	0.8
11	68.1	20.1	34.8	19.0	26.4	0.8
8	77.4	25.2	38.8	30.6	35.6	0.9
8	76.7	24.8	39.0	26.3	31.2	0.8
8	91.7	33.2	43.4	30.1	34.2	0.8
8	92.8	33.8	52.5	25.5	34.5	0.7
7	97.7	36.5	29.4	27.7	29.6	1.0
9	96.6	35.9	35.2	24.4	27.9	0.8
6	102.6	39.2	14.5	27.4	18.6	1.3
6	102.0	38.9	12.6	25.2	20.6	1.6

The fact is clear in Table 7 that at temperatures ranging from 7.0° to 68.1°F. (—13.9° to +20.1°C.), the heavier birds lived, on the average, the longer time, although the differences do not amount to more than a few hours. Schimanski (1879) and Chossat (1843) obtained similar results. This would be expected because the heavier birds have, supposedly, a greater

reserve supply of food, probably in the form of fat. The heavier birds lose a relatively greater total percentage of their original weight before death occurs, which would indicate that the extra weight is in the form of reserve food material. There is a slight tendency for the percentage of the weight lost per hour to be higher in the heavier birds and this counteracts, to some extent, the value of the bird's greater surplus of weight.

At the air temperature of 76.7° to 77.4°F. (24.8° to 25.2°C.) a marked difference in body weight produces a negligible difference in survival time. At higher temperature ranges of 91.7° and 97.7°F. (33.2° and 36.5°C.), birds of greater weight live a shorter time than do those of lighter weight, which is just the reverse of what happens at lower temperatures. The rate of metabolism and water loss, as indicated by the percentage weight lost per hour, is higher in the heavier birds than in the lighter, which is the same relation that holds at lower air temperatures. At these high air temperatures, the higher rate of metabolism in heavier birds becomes critical because of the great difficulty of dissipating the surplus heat with sufficient rapidity over the limited surface areas of the body, lungs, and air-sacs to prevent accumulation of this heat within the body. This raises the body temperature and causes other physiological disturbances. The ability to lower the rate of metabolism is as much an advantage at high air temperatures as the raising of the metabolism is of advantage at low air temperatures.

At a temperature of 102°F. (38.9°C.), heavier birds in these experiments again survived for a longer period than did the lighter birds. In this case, however, for some reason not entirely clear, the heavier birds had a decidedly lower rate of percentage weight lost per hour, and this would serve to explain the unexpected results. It is barely possible that, at these unusually high air temperatures, a fat body may serve in some way as an added insulation against external temperatures so that the rate of metabolism is not so readily affected.

*Effect of age and sex on survival time*—Juvenile English sparrows were caught in large numbers in the bird traps while adult birds were difficult to secure. Records on only eleven adults are included in the data presented, while all the other records were obtained on juvenile birds of the year. The juvenile birds in all cases were a few weeks, at least, off the nest, since they were well able to take care of themselves. In a study of the physiology of temperature in passerine species (Baldwin and Kendeigh 1932) it has been shown that in the house wren, temperature control is established nine days after hatching. It is not at that time as perfect as in the adult but gradually becomes so. The young birds are taken care of by the adults for at least two weeks after they leave the nest. By the end of that time their temperature resistance should be as perfect as in the adults. In Table 8 a comparison is made of the survival time of juvenile and adult English sparrows as far as the records permit.

TABLE 8—Comparison of survival time of adult and juvenile English sparrows without food at different air temperatures. Birds were kept in darkness with temperature and relative humidity constant.

ADULT BIRDS				JUVENILE BIRDS			
Number of birds	Average temperature		Survival time: hours	Number of birds	Average temperature		Survival time: hours
	°F.	°C.			°F.	°C.	
1	8.0	—13.3	12.5	12	6.9	—13.9	11.3
2	14.2	— 9.9	7.9	6	13.1	—10.5	10.7
2	33.4	0.8	14.1	14	35.0	1.7	18.4
2	65.8	18.8	23.8	16	67.9	19.9	37.3
2	97.8	36.6	21.9	14	97.0	36.1	34.1
2	101.0	38.3	17.8	10	102.6	39.2	12.8
11	....	....	(Ave.) 16.2	72	....	....	(Ave.) 20.8

Adult birds are not able to survive without food a longer time than juvenile birds. There was no significant difference in the average body weight of the adult and juvenile birds. It is permissible, therefore, to use the records obtained, largely on juveniles, to represent the species as a whole. Riddle, Smith, and Benedict (1932) did not find any difference in the rate of metabolism of mourning doves, *Zenaidura macroura carolinensis* (Linnaeus), in the winter between individuals from six to fifty months of age.

No extensive study on the effect of sex upon the survival time of English sparrows has been made, largely because of the difficulty of securing adult birds. The few records available do not indicate any significant sex difference. A difference between the sexes in survival time may very well exist in some other species where there is a pronounced difference in weight, but such a difference, if it occurs, could be explained better by the difference in weight than by any gonadal influence in itself. A marked difference between sexes in rate of metabolism would also, presumably, affect survival time.

*Effect of relative humidity on survival time*—The relative humidity in these experiments was not controlled and varied inversely with the air temperature. In a general way this was desirable because under natural conditions relative humidity varies inversely with temperature to a comparable extent. The lowest relative humidity during the day ordinarily comes near noon or shortly after when the air temperature is the highest; while the relative humidity approaches saturation at night when the air temperature is low. The relative humidity during the experiments conducted at 7.0°, 13.6°, and 24.3°F. (—13.9°, —10.2°, and —4.3°C.) was not measured but was probably over 90% and approaching saturation. At low air temperatures, moist air generally increases the sensitivity of an organism to cold, because it increases the heat conducting capacity of the air. With mammals and men possessing sweat glands, a high relative humidity lowers the tolerance to high air temperature, because it prevents rapid evaporation of sweat. As birds do not

possess sweat glands, it was desirable to determine how they would react to different combinations of relative humidity with high air temperature. Kayser (1930) found that when placed at 86.°F. (30°C.) the metabolism of pigeons was higher and the moisture output through the lungs was lower in humid air than in dry air.

In the experiments for testing the effect of relative humidity on the survival time of English sparrows at high air temperatures, an incubator was used. The relative humidity was increased by the insertion into the incubator of three small dishes of water with soaked paper towels in them to increase the surface for evaporation of water. The relative humidity was decreased by simply removing all traces of water from the incubator. The relative humidity was measured by means of a small precision hair hygrometer, carefully checked beforehand. The results are shown in Table 9. From this

TABLE 9—*Survival time of English sparrows placed in different relative humidities at high air temperature. The birds were kept in darkness, without food, and at a constant air temperature.*

Number of birds	Air Temperature		Relative humidity: percent.	Survival time of birds: hours	Average initial weight of birds: grams	Total percentage of initial weight lost at death	Percentage of initial weight lost per hour
	°F.	°C.					
8	104.0	40.0	77.1	3.3	27.4	8.0	2.4
6	105.1	40.6	20.5	6.8	26.7	17.6	2.6

it appears that a high air temperature is tolerated less effectively by birds when the relative humidity is high than when it is low. The influence of the relative humidity of the air must be exerted by modifying the evaporation of moisture in the bird's lungs, thereby affecting the temperature-regulating mechanism.

A consideration of Table 3 from the basis of the experiment just described indicates that the values given for the survival time at high air temperatures may be greater than they would have been had relative humidities comparable to those run at the lower temperatures been used. Lower relative humidities than those used at the lower air temperatures would have presumably lengthened the survival time at those temperatures also, but it is doubtful if the difference in either case would have produced very great changes. The effect of temperature is so obviously profound, that any effect of relative humidity must be considered a secondary factor. The modifying effect of relative humidity under natural conditions would be most important when air temperatures became extreme. A high humidity would tend to lower the degree of high air temperature that first became critical and to raise the degree of low air temperature that first became seriously detrimental.



*Effect of light on survival time*—In practically all the experiments thus far reported, the birds were kept without food in constant darkness, because this best simulated natural conditions out-of-doors, where the birds are subjected to low temperatures at night. In the experiments here reported, the birds were kept in continuous light supplied by artificial illumination. Table 10 indicates that the survival time of birds kept in continuous light is less than when they are confined to complete darkness. This effect of light is particularly important at high air temperatures because high air temperatures occur under natural conditions in the middle of the day.

TABLE 10—*Effect of constant light upon survival time of English sparrows without food.*

Number of birds	Average air temperature		Condition of light	Survival time: hours	Initial weight: grams	Total percentage of initial weight lost	Percentage of initial weight lost per hour
	°F.	°C.					
15	66.2	19.0	Light	28.3	30.3	34.7	1.2
18	67.7	19.8	Dark	35.8	27.4	28.1	0.8

The reason for the shorter survival period of birds in the light as compared with darkness is that the birds are more active and restless and, as a consequence, expend more energy. In the dark, the expenditure of energy is at a minimum because activity is limited. The greater metabolism of active birds is indicated by the much larger percentage of initial weight lost per hour. The reserve food supply in the body is used more rapidly and so death occurs sooner. These results are supported by those of Benedict and Riddle (1929) who measured the metabolism of ring doves in the light and dark and found it to be decidedly greater when the birds were in the light.

*Effect of wind on survival time*—Under natural conditions, birds are frequently subjected to movements of air of greater or lesser velocity, and so it is of interest to determine what effect a moderate breeze has upon survival time. In the experiments, a current of air from a small electric fan two feet away from the cages was directed at the birds. No instruments were available at the time to measure the velocity of the breeze produced, but it was moderate, as the copper screen of the cages intercepted much of it before it reached the birds inside. The birds subjected to the breeze lived a considerably shorter period than did those in undisturbed air (Table 11.) The rate of metabolism was higher, weight was lost more rapidly, and death came sooner. The effect of the breeze upon the birds was about the same as lowering the air temperature in still air about 28°F. (15.6°C.). A breeze carries the body heat of the bird away faster, and gets in between the feathers and increases the conductive capacity of the air. At the same time the breeze may have been instrumental in causing greater activity on the part of the bird.

TABLE 11—*Effect of a moderate breeze on the survival time of English sparrows without food and in the dark.*

Number of birds	Average temperature		Breeze	Survival time: hours	Initial weight: grams	Total percentage of initial weight lost	Percentage of initial weight lost per hour
	°F.	°C.					
12	66.9	19.4	With	22.8	27.4	24.8	1.1
18	67.7	19.8	Without	35.8	27.4	28.1	0.8

*Effect of natural conditions on survival time*—In order to determine whether birds would live longer out-of-doors where they would be subjected to natural fluctuations in temperature, humidity, light, and wind, birds were confined in somewhat larger cages and placed outside. They were here protected from the full effect of the sun and rain but exposed to natural fluctuations in other environmental factors. The results are given in Table 12, where the survival time of these birds is compared with that of birds under controlled and constant conditions indoors.

TABLE 12—*Effect of natural fluctuations in temperature, relative humidity, wind, and light on the survival time of English sparrows without food.*

Number of birds	Average temperature		Survival time: hours	Initial weight: grams	Total percentage of initial weight lost	Percentage of initial weight lost per hour
	°F.	°C.				
19	68.7	20.4	27.5	28.1	28.1	1.0
Control—temperature, humidity, and darkness constant, no wind.						
18	67.7	19.8	35.8	27.4	28.1	0.8

Fluctuations in air temperature, as already shown, do not appreciably affect the survival time of birds. The full importance of the relative humidity factor is not yet clear, but the belief is that survival time at a fluctuating relative humidity would not be greatly different from what it would be at a constant relative humidity of a mean percentage. The wind factor was of some importance, although the birds were not exposed to very much breeze during the course of the experiments. The birds were in the light during the normal day period and in the dark at night, and, as light decreases the survival time of birds without food, it may be that the light factor was the most important one in the experiment causing the decrease in survival time.

In another experiment, five birds were placed under natural conditions similar to those obtained during the previous experiments but with an electric

fan directing a moderate constant breeze upon the birds. The survival time of these five birds was thereby shortened to 18.5 hours.

*Effect of season (winter) on survival time*—In order to test the resistance or survival time of birds in the winter as compared with the summer, an extensive study was made with the English sparrow during the winter months of December, January, February, and early March in as nearly the same way as during the summer as was possible. The same instruments and cages were used, and observations were made in a similar manner. The results of this series of experiments are given in Table 13. The total number of records

TABLE 13—*Survival time of English sparrows in winter at different air temperatures under controlled conditions. Birds kept in darkness without food.*

Number of records	Average temperature		Survival time: hours	Initial weight of birds: grams	Total percentage of initial weight lost	Percentage of initial weight lost per hour
	°F.	°C.				
4	5.2	-14.9	21.4	29.4	17.3	0.8
6	14.7	-9.6	20.5	29.8	20.1	1.0
3	27.9	-2.3	20.5	29.4	13.9	0.7
5	32.6	0.3	23.7	29.5	16.9	0.7
11	71.9	22.2	63.3	29.1	34.0	0.5
4	86.8	30.4	72.5	30.3	36.6	0.5
6	92.3	33.5	76.1	30.8	39.3	0.5
4	96.6	35.9	44.5	29.8	30.9	0.7
4	101.1	38.4	9.9	29.5	13.2	1.3

for the different temperatures are not as great as might be desired because of the difficulty experienced in capturing sparrows during the winter months. The results obtained nevertheless are consistent throughout.

A comparison of the survival time of English sparrows in the winter with their survival time in the summer is made in Figure 8. The general shape and character of the winter curve of survival time is similar to that of the summer-curve which has already been explained in detail. The much greater survival time of birds in the winter over that in the summer is apparent. The survival time in winter, between the temperatures of 0° and 95°F. (-17.8 and + 35.0°C.) averages 63% longer than in summer.

At air temperatures below 30°F. (-1.1°C.), the survival curve of winter birds (Fig. 8) flattens out. The survival curve of summer birds does not flatten out until below 15°F. (-9.4°C.). Just how low air temperatures can be tolerated by English sparrows, these experiments do not show. However, they do show that, even in winter, English sparrows are unable to endure temperatures below 32°F. (0.0°C.) without food for 24 hours.

The sharp break in the survival curves for both winter and summer comes between 90° and 95°F. (32.2° and 35.0°C.) air temperature. This is apparently an upper critical air temperature range of considerable significance.

Above this point, survival time decreases at a very fast rate. The effect on winter birds of air temperatures of 100°F. (37.8°C.) and above appears to be more severe than on summer birds, since their survival time is shorter.

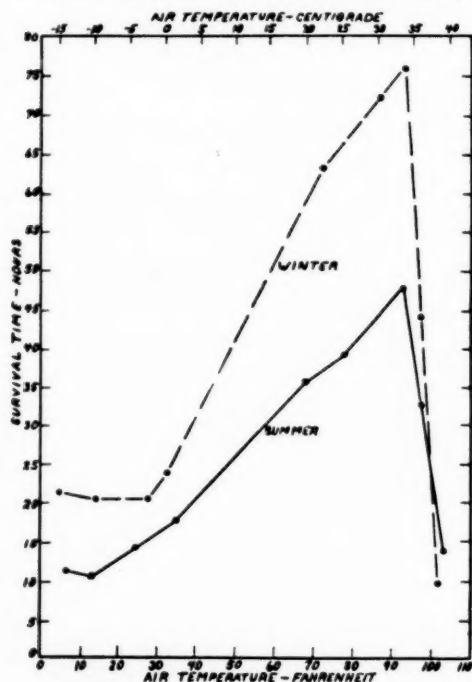


FIG. 8. Difference between summer and winter in the survival time of English sparrows without food at different air temperatures.

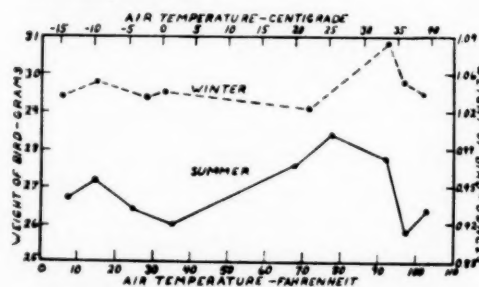


FIG. 10. Difference between summer and winter in the body weight of English sparrows used at different temperatures in experiments on survival time without food.

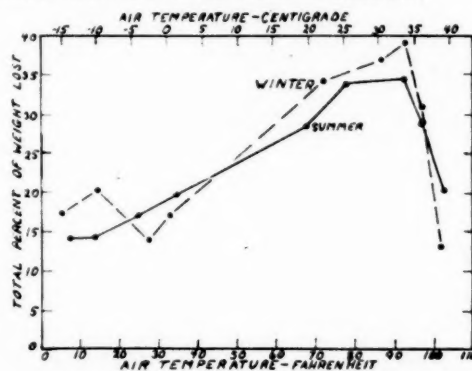


FIG. 9. Difference between summer and winter in the total percentage of the initial body weight lost at time of death by the English sparrow when confined without food in the dark at different air temperatures.

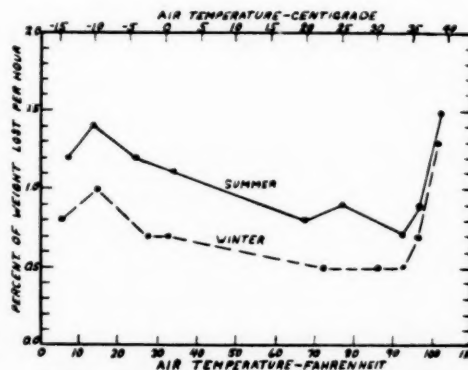


FIG. 11. Difference between summer and winter in the percentage of the initial body weight lost per hour by the English sparrow when confined without food in the dark at different air temperatures.

The total percentage of original body weight lost before death is not consistently higher or lower in summer or winter birds (Fig. 9), although, at air temperatures between 68° and 97°F. (20.0° and 36.1°C.) and again at temperatures below 15°F. (-9.4°C.), there is a greater percentage loss in winter birds than in summer. This may be partly responsible for the much longer survival time of winter birds in these ranges of air temperature, since



it would infer that a greater percentage of the body weight was in the form of fat. Above 100°F. (37.8°C.), winter birds die more quickly than do summer birds without losing correspondingly so much body weight.

In order to gain additional information on whether or not winter birds possess more food reserves in the body, the initial weights of summer and winter birds are compared (Fig. 10). The average weight of the winter birds used at each degree of temperature was everywhere greater than the average weight of the summer birds. Other available data that cannot be incorporated in the present paper indicate that this same weight relation between summer and winter may be generally true for passerine species. The fact that English sparrows and other passerine species weigh more in winter than they do in the summer presumably is due to their freedom from the cares and activities of reproduction, freedom from the exhaustive process involved in molting which occurs in late summer, and probably to physiological changes that accompany changes in the climatic environment. Groebbs (1930) attempts to explain the increase in weight of birds in the autumn by changes in the endocrine organs, particularly the gonads and thyroids, whereby anabolism becomes more rapid than katabolism. Linsdale and Sumner (1934) have shown recently that an inverse correlation between air temperature and body weight may occur even from day to day.

A comparison between summer and winter birds in the percentage of original body weight lost per hour shows clearly (Fig. 11) that, at all degrees of air temperature, winter birds lose weight much more slowly than do summer birds. The rate of metabolism of winter birds at the same degree of air temperature is less, therefore, than that of summer birds. This is particularly true at air temperatures below the upper critical temperature of 93.0°F. (33.9°C.). From actual measurements of metabolism Riddle, Smith, and Benedict (1934) found this lower winter rate to hold also for tumbler pigeons. This must be the reason, in large part, why winter birds survive at the same air temperature a longer time than do summer birds.

In attempting to analyze the cause of the lower rate of metabolism in winter birds a study was made of seasonal variations in the density and thickness of the bird's feather covering. A thicker or heavier plumage should, theoretically, give the bird a greater protection against cold than a lighter plumage, thereby permitting a lower metabolism for maintaining the body temperature. With the house wren the feathers must be fluffed out to prevent the temperature regulation of the body from being broken when the air temperature falls to 50°F. (10°C.) (Baldwin and Kendeigh 1932). Buckard, Dontcheff, and Kayser (1933) have also shown that if a pigeon is prevented from fluffing out its feathers when placed at low air temperatures there is an extra strain on its body metabolism, as heat production must be higher to maintain a constant body temperature. Wetmore (1921), in his study of

the temperature of birds, suggested that the plumage of birds may be heavier during the winter than during the summer to give added heat protection but he made no special study of the problem. Mayer and Nichita (1929) found that the metabolism of rabbits was lower in winter than in the summer at identical air temperatures, which is similar to our findings with birds, and they were able to correlate this definitely with heavier fur on the animals during the winter season.

In obtaining the weight of the bird's plumage, the following method was employed. The bird, recently killed, was weighed with feathers intact. The feathers were then stripped off as thoroughly and as cleanly as possible from all over the body. The remiges and retrices were separated from the rest of the feathers, since they function primarily for flight and not for body insulation. The remaining feathers were weighed immediately, and the percentage of this weight to the total weight of the bird was determined. Magnan (1911) used a somewhat similar method for estimating the quantity of feathers on 55 species of European birds, although he weighed the bird both before and after stripping it of feathers and used the difference as the weight of the feathers. He did not separate the flight feathers from those of the rest of the body, nor did he make any study of seasonal variation in the weight of feathers.

From Table 14 it is evident that the weight of the plumage in many species of birds is heavier in the autumn, both actually and relative to the total body weight, than at any other season of the year. This is, of course, immediately after the annual molt that occurs late in the summer and early autumn. There is a gradual decrease in the weight of the plumage during the winter, spring, and summer caused by loss and abrasion of feathers. This gradual loss in plumage weight through the year may not, however, be true in species having a more or less complete spring molt.

The weight of the plumage of adult English sparrows is 28.9% greater by actual weight in the winter than it is in the summer. The weight of the plumage of adult English sparrows in the winter is 90% greater by actual weight than is the plumage of juvenile birds in the summer. This means that the insulation against cold and the heat retaining capacity of the body is much greater in the winter than in the summer. Another factor tending to better insulate the body against cold in the winter is the surplus weight in the form of fat. This is usually present in layers just underneath the skin and is, of course, very important in preventing too rapid radiation of heat from the body.

A greater insulation of the bird with feathers and fat explains, in large part, the longer resistance against death by starvation of birds in the winter at medium degrees of air temperature. It undoubtedly also enables the bird to withstand a much lower air temperature in the winter than in the summer,



which ability is indicated in Figure 8. The English sparrow in winter can certainly resist air temperatures several degrees below  $0^{\circ}$  ( $-17.8^{\circ}\text{C}.$ ) but not for an indefinite number of hours. That the English sparrow is unable to resist similar low air temperatures during the summer is evident from the much closer approach of the summer curve of survival time to the zero base line at air temperatures below  $10^{\circ}\text{F}.$  ( $-12.2^{\circ}\text{C}.$ ).

Another factor that may be involved in giving birds a resistance to extremely low air temperatures in the winter is a potentially more active endocrine system and the ability, when necessary, to increase greatly the rate of metabolism or heat production in the body. The regulation of heat production in the body is an involuntary function, controlled in large part through endocrine action (Baldwin and Kendeigh 1932). The necessity for a rapid metabolism and consequently more rapid utilization of reserve food supplies is generally avoided at medium winter air temperatures by the substitution of a better insulating coat of feathers and fat. A greatly increased rate of metabolism in order to maintain the body temperature would be advantageous and necessary only during periods of unusually low air temperature. With this idea in mind, a special study has been begun of the rôle played by the thyroid gland in wild birds in maintaining resistance against low air temperature at different seasons of the year, because the general function of a high rate of hormone secretion from the thyroid gland is well known to be correlated with a greatly increased rate of metabolism, while a low rate of secretion is correlated with a much reduced rate of metabolism. Riddle and Fisher (1925) and Haecker (1926) have already produced some evidence that the thyroid in birds may be more active in the colder months of the year.

The lesser resistance of birds in the winter to extremely high air temperature needs some consideration. If the upper extremities of the survival curves in Figure 8 are extended to the zero base line, it would be apparent that birds in the summer are able to withstand, for short periods of time, air temperatures  $5^{\circ}\text{F}.$  ( $2.8^{\circ}\text{C}.$ ) or more higher than can birds in the winter. A heavy coat of feathers and a thick layer of fat, while serving for better protection of birds in the winter against low air temperature, are at the same time detrimental at extremely high air temperature because they diminish the radiation of excess heat from the general body surface. As a consequence of this the body temperature rises sooner and more rapidly, and fatal results quickly occur. Riddle, Smith, and Benedict (1934), studying seasonal changes in the metabolism of pigeons, found that the birds are more sensitive to high temperature in the autumn and winter, when out-of-doors temperature is low, than they are in the summer. Kayser (1929) had earlier found that pigeons are subject to more change in metabolism at a high air temperature when they had previously been subjected to cold for several days than when they had previously lived at a higher air temperature.



*Temperature resistance of the eastern house wren*—All the detailed preliminary work analyzing the factors involved in the temperature resistance of birds was performed with English sparrows. A comparison of the survival time of the English sparrow with the survival time of the house wren, however, is necessary in carrying this study further. That the curve of survival time at different air temperatures is of the same general nature with the house wren as with the English sparrow is indicated in Figure 12, which is based, however, on only 11 records at 5 different temperatures.

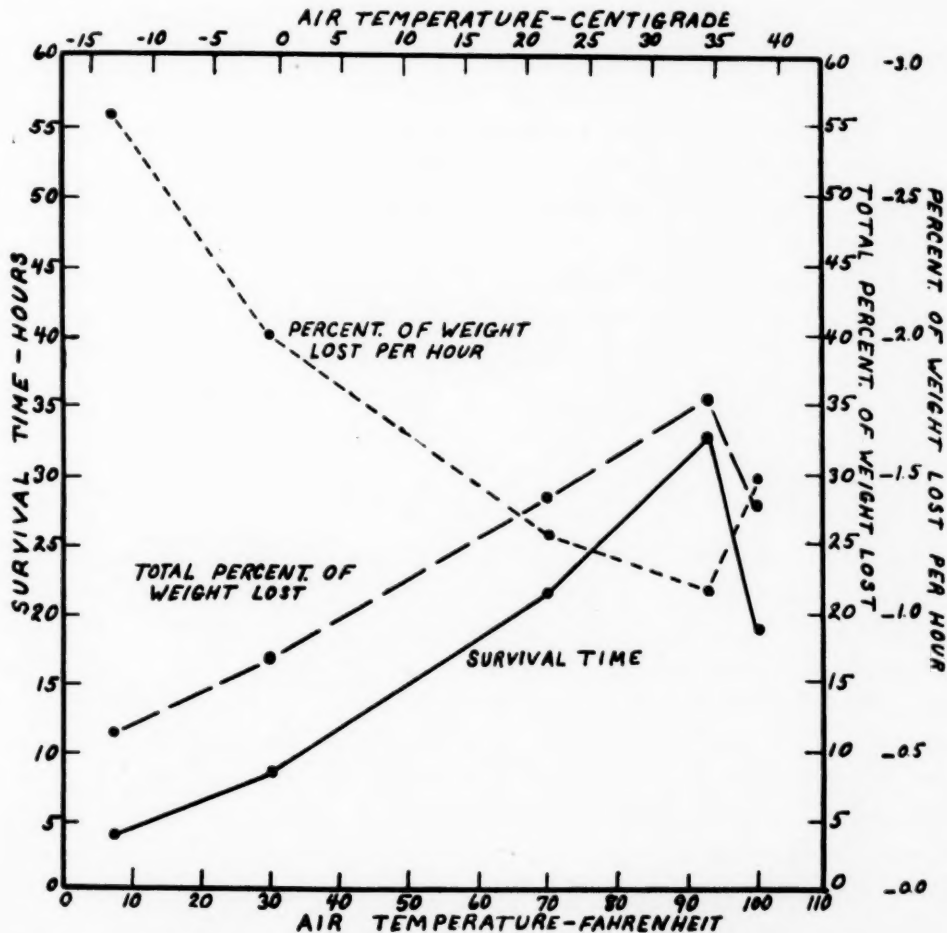


FIG. 12. Variation at different air temperatures of the survival time of eastern house wrens without food, of the total percentage in the initial body weight lost at time of death, and of the percentage in the initial body weight lost per hour.

A comparison of Figure 12 with Figure 5 is interesting when it is borne in mind that the house wren is a summer resident only, while the English sparrow remains as a permanent resident throughout the year. At a temperature of 32°F. (0°C.), the English sparrow has nearly twice the survival time of the house wren. The difference in total percentage lost in body

weight at time of death between the two species is probably insignificant. The percentage weight lost per hour is very much higher in the house wren. This is of considerable importance when taken with the fact that the body weight of the house wren is less than half that of the English sparrow. It may mean that the rate of metabolism in the house wren is considerably higher than in the English sparrow and that reserve food supplies in the body are utilized with corresponding rapidity. Interesting differences of this nature in metabolism and temperature resistance may exist between many species of birds.

Riddle, Smith, and Benedict (1932) make the suggestion, as the result of comparing the rate of metabolism of the ring dove and common pigeon (non-migratory species) with the mourning dove (a migratory species), that the thyroids of species that migrate may not respond to the onset of cold weather by increased activity, while those of species that do not migrate do respond, and that this difference may be fundamental in the resistance of species to cold. They also found that the rate of metabolism in the mourning dove is higher than is that of the other two species, indicating that at identical low temperatures this migratory species must do more work and produce more heat in order to maintain its body temperature than is necessary for the non-migratory species. This distinction is apparently true also between the English sparrow and house wren.

The resistance time of house wrens recently arrived from the south in spring migration is 1.2 hours longer at the same temperature ( $31.0^{\circ}\text{F.}$ ,  $-0.6^{\circ}\text{C.}$ ) than of birds in the middle of summer. This correlates with the fact that the weight of the body plumage of 10 birds in late spring averaged 523 milligrams or 4.7% of the total body weight, while the weight of the body plumage of 13 birds in the middle of the summer averaged only 390 milligrams or 3.5% of the total body weight. For the range in air temperature from  $0^{\circ}$  to  $32^{\circ}\text{F.}$  ( $-17.8$  to  $0.0^{\circ}\text{C.}$ ), the English sparrow in winter increases its resistance time approximately 59% over what it is in the summer. If the house wren could increase its own resistance to a similar extent, its survival time in winter at  $32^{\circ}\text{F.}$  ( $0.0^{\circ}\text{C.}$ ) would be only about 14 hours.

A comparison of the resistance of the two species to a high temperature of approximately  $100^{\circ}\text{F.}$  ( $37.8^{\circ}\text{C.}$ ) shows that in the middle of the summer the house wren has a shorter survival time; the survival time being 19.4 hours in the house wren and 23.0 hours in the English sparrow. Likewise, the percentage of initial weight lost per hour in the house wren is 1.5, in the English sparrow 1.2. In late May and early June, soon after arrival from the south, the survival time of the house wren is only 9.0 hours and the percentage weight lost per hour is 2.4. This lesser resistance of the house wren to a high air temperature in spring over the resistance in the middle of

the summer, substantiates the lesser resistance also of English sparrows in the winter over that in the summer.

*Critical rôle of temperature*—On the basis of the experiments and results just discussed, it is apparent that the critical aspect of low air temperature consists not in the absolute degree of low temperature itself, but low temperature combined with a period of time in which the bird must remain without food. Night-time is, therefore, involved in a very important manner. In considering the critical rôle of temperature as it affects the behavior, distribution, migration, and abundance of birds, the *average night temperature* in conjunction with the *number of hours of darkness* appear to be the important factors.

In the case of some of the larger birds of greater weight and correspondingly greater food reserves in the body, the critical rôle of night temperature and hours of darkness may become effective only if accumulative over a long period. If a bird is able during the daytime to assimilate only a part of the equivalent total energy that it loses at night, there will finally come a time when its temperature tolerance entirely breaks down, which results in death.

Groebbels (1927, 1928, 1930, 1932) has arrived at similar conclusions concerning the rôle of temperature, although he emphasizes duration of daylight rather than night and does not stress night temperature as such. Rowan (1931) is primarily concerned with the direct regulatory effect of the gonads upon bird migration, yet he realizes the importance for the bird of acquiring sufficient food during the short daylight hours of midwinter to maintain its requirements. He believes that there are certain latitudes in the winter where this cannot be accomplished by some species.

From our study of the physiology of bird temperature, it appears that the critical time of the day when *high* air temperature may first become effective is during the daylight hours, usually in the early afternoon. At this time, the maximum points are reached in the daily rhythm of both bird and air temperatures. High air temperatures may have as great or greater an indirect influence on the bird by affecting its activity and the rate of metabolism in the body than directly by causing a harmful rise in body temperature. Riddle, Christman, and Benedict (1930) maintain that even at 86°F. (30.0°C.) metabolism of ring doves becomes so depressed that the birds are in an abnormal physiological condition. In the experiments on temperature resistance reported in this paper, it was shown that the rate of metabolism reaches a minimum at an air temperature of 93°F. (33.9°C.) Lower temperatures of the air stimulate metabolism and induce greater activity on the part of the bird. Higher air temperatures cause a great loss of moisture through the lungs and may also raise the metabolism but too rapidly and to the detriment of the bird. A temperature of 93°F. (33.9°C.) may, therefore, be considered a critical

point. Activity is curtailed at this temperature, along with metabolism, since the least exertion causes an undesirable rise in body temperature. Normal behavior and reproduction are, therefore, interfered with. Survival is possible for several hours at an air temperature above the upper critical point, but such existence is increasingly uncertain and undoubtedly very uncomfortable. The fact that under natural conditions, birds are in daylight when these high temperatures are reached rather than in darkness, as in our experiments, may actually hasten the harmful effect of high air temperature and lower the degree to be considered the upper critical temperature. The evidence indicates, therefore, that the critical rôle exerted by high air temperature is played by the *daily maximum temperature*.

*Summary of experiments on temperature resistance in birds*—In order to organize and correlate the work performed in the study of temperature resistance, the following summary is given which will furnish the basis for discussion later in the paper:

1. Adult passerine birds have considerable resistance for short periods to low air temperatures even though these may be extreme. A body temperature down to 75°F. (23.9°C.) may sometimes be endured for brief periods, although a body temperature below 102.0°F. (38.9°C.) is abnormal.

2. High air temperatures (95°F., 35.0°C., or above) have a more immediate, and possibly fatal, effect upon birds than low air temperatures. The margin of safety between the highest body temperature normal to birds (112.3°F., 44.6°C.) and the lethal body temperature (116°F., 46.7°C.) is very small.

3. Night time is the most significant period of the day for birds in their tolerance to low air temperature because at that time the daily rhythm of both body temperature and body metabolism reaches the lowest point, the birds are without food for several hours, the birds must remain largely inactive, and it is at this time that air temperature also ordinarily reaches its lowest point during the day.

4. The most important period of the day in the resistance of birds against high air temperature is usually in the early afternoon, as it is at this time that the maximum is reached in the daily temperature rhythm of both the bird and the air.

5. The survival time of passerine birds confined in darkness and kept without food (to simulate natural conditions at night) varies with the air temperature, being longest at a medium high air temperature (93°F., 33.9°C.) with the English sparrow and house wren and being progressively shorter at both lower air temperatures and extremely high air temperatures.

6. These differences in survival time of birds at different air temperatures are explained by differences in rate of metabolism and water loss. The rate of metabolism increases with a decrease from medium high to low air



temperature and this exhausts the reserve food supplies in the body more quickly. Water loss through the lungs increases considerably with a rise in air temperature from medium to extremely high air temperatures, but this does not prevent an eventual breakdown of the body temperature regulation.

7. There is considerable variation in survival time between individuals of the same species. Heavier birds live longer than do lighter birds at low air temperatures but not so long at high air temperatures. No significant difference in the length of the survival period due to differences in age was noted.

8. There is a marked seasonal variation in the length of the survival period within the same species. Birds in winter live considerably longer at identical medium and low air temperatures than do birds in summer and are able to endure several degrees lower air temperatures. The resistance of birds in winter against extremely high air temperatures is less, however, than that of birds in the summer.

9. The apparent underlying reasons for a seasonal difference in temperature and starvation resistance by birds are the greater weight of the birds in the winter because of greater food reserves in the body, the greater covering of feathers and fat which reduces the amount of metabolism necessary to maintain the body temperature, and probably also the potentially greater activity of the thyroid gland.

10. Whether medium air temperatures are constant or fluctuating makes no difference in the survival time of birds without food.

11. A high relative humidity decreases the survival time of birds at high air temperatures.

12. The survival time of birds is reduced when they are kept in the light. The reason for this is that in the light the birds are more active and, consequently, more rapidly diminish their reserve food supplies.

13. The survival time of birds subjected to a modern breeze or wind is shortened on account of the cooling effect and possibly greater activity produced.

14. The survival time of birds without food exposed to natural fluctuations in light and darkness, humidity, wind, and temperature is not greater than expected from an analysis of the effect of these factors under controlled experimental conditions.

15. Temperature resistance as measured by length of survival time in darkness without food varies between species at both low and high air temperatures. This is explained in part by differences in body weight and rate of metabolism.

16. The critical factor involved in the resistance or tolerance of small passerine birds to cold is average night air temperature combined with num-

ber of hours of darkness. The critical factor involved in the tolerance of birds to heat is the daily maximum air temperature.

#### BEHAVIOR RESPONSES

In this section an attempt will be made to estimate the extent to which air temperature influences the natural life-history behavior of birds. The preceding sections of this paper have been concerned with the physiology of temperature resistance in birds and with the adjustment of the bird physiologically to external temperature conditions. The present concern is with how the bird adjusts its life-history behavior to meet external conditions. These adjustments must be, of course, compatible with the physiological possibilities of the bird and must be limited and conditioned by them.

*Activities at night*—Most passerine species are inactive at night except for slight movements in changes of position. During the breeding season, the female house wren spends every night on the nest from the time the nestling first goes in until the young are nearly ready to leave the nest fifteen days after hatching. In this way, the female keeps the eggs and young birds warm and is also in a sheltered place herself. The female probably behaves similarly in most passerine species. Although the male house wren builds "bachelor" nests in addition to the one where the female is active, he never spends the night in these nests. His roosting place is frequently in some cranny or corner of some building or in a thick vine or bush. This furnishes some shelter from wind and the cold. Two house wrens kept in captivity roosted close together all night on a perch near the top of the cage. During late summer and fall, house wrens are frequently found in piles of dead brush and presumably they spend the night there.

Other species of birds have other habits of passing the night. Comparatively little is known about the night behavior of birds. A tufted titmouse, *Baeolophus bicolor* (Linnaeus), was once observed at dusk to go into a space between a piece of loose bark and the trunk of a tree lying horizontally across a small stream. All indications were that the bird intended passing the night there. According to Allen (1928), black-capped chickadees, *Parus a. atricapillus* (Linnaeus), also pass the night in natural cavities of trees, while brown creepers, *Certhia familiaris americana* Bonaparte, cling head upward in depressions of the trunk. Woodpeckers roost in holes in trees. The northern downy, *Dryobates pubescens medianus* (Swainson), and eastern hairy woodpeckers, *Dryobates v. villosus* (Linnaeus), actually chisel out holes in decaying limbs in the fall to make sheltered roosting places, similar to the holes that they use for nesting purposes in the summer. English sparrows may roost singly or in small groups. They may be found frequently in vines next to buildings, in thick bushes, or in buildings. Allen (1928) says that tree sparrows, *Spizella arborca* (Wilson), stay over night during winter

in broken down clumps of cattail and clumps of grass in frozen marshes. Song sparrows, *Melospiza melodia* (Wilson), frequent low bushes, while slate-colored juncos, *Junco h. hyemalis* (Linnaeus), are frequently found in evergreens. Prairie horned larks, *Otocoris alpestris praticola* Henshaw, sleep under the shelter of clumps of grass or clods of dirt (Pickwell 1931). Large roosts of eastern robins, *Turdus m. migratorius* Linnaeus; bronzed grackles, *Quiscalus quiscula aeneus* Ridgway; starlings, *Sturnus v. vulgaris* Linnaeus; or eastern crows, *Corvus b. brachyrhynchos* Brehm, during the fall and winter are of common occurrence. Here large numbers of individuals may gather and spend the night together in fairly close quarters in thick trees.

Most birds sleep with their head turned back and buried in the feathers of the shoulder and wing. In this way the neck muscles may be relaxed and the eyes protected from the cold. A few species, as the mourning dove, merely draw in the head and bury the bill in the feathers of the neck.

Much more needs to be learned about the night habits of birds, particularly in winter. What is known indicates that, in general, birds seek out places sheltered from the wind and snow. If the place is small and partly enclosed, the heat radiation from the bird itself may be sufficient to raise the temperature of the surrounding air by several degrees so that the bird is not actually subjected to what may be intense cold outside. It has been our observation also that at night birds commonly fluff out the feathers all over their body. This increases the thickness of their insulating coat against the cold and is an important factor in their toleration of low temperature. Another point that is worthy of notice is that the roosting of large numbers of birds in close compact groups conserves the body heat and the birds help to keep each other warm. The behavior of birds at night, therefore, is adjusted to help tide them over this critical period.

*Activities during the day*—Birds are usually able to withstand low temperature during the day as long as they can obtain a sufficient amount of food and can remain active. Activity, when food is available, is a great asset during cool weather because it aids in maintaining body temperature. Lorenz (1932) has described how swallows in Europe sleep soundly during the daytime in close dense groups when food is not available and the weather is cold and wet. He believes this is distinctly advantageous to the birds for passing through short unfavorable periods, because their metabolism is lowered and consequently their survival period is lengthened. Our own experiments (Table 10) support this, because they show that quiet birds survive without food a longer time than active birds.

As a rule, birds are more active during cool weather than when it is hot and humid. Hancock (1911) narrates in a fine descriptive manner the effect of July heat on depressing the activity and comfort of indigo buntings,

*Passerina cyanea* (Linnaeus), and robins, and says that bob-white, *Colinus v. virginianus* (Linnaeus), leave the fields during these periods to seek the shelter of forest-edges. It is a general observation that eastern robins seek the woods in large numbers in late July and August, although during the cooler spring weather they are seldom found there. Birds sing more on cool days when there is little rain. Very hot weather or heavy winds silence them. Cloudy weather, since it affects the temperature by lowering it, is favorable to song (Saunders 1929). Palmgren (1932) has used a quantitative method for measuring the amount of singing by birds at different times of the day and finds that it varies inversely with air temperature. On the hot prairies and deserts of western United States, birds are more active and sing most during the cool morning and evening hours, while during the middle of the day they become silent. The same is less pronounced in the more temperate eastern part of the country. Groebbels (1925) believes that this early morning singing is a direct response to the then prevailing lower temperatures. During the last of July and August, birds are not much in evidence and, except for a few species, are mostly quiet. This may be due to a natural retirement of the birds during the molting season, but also coincides with the highest temperatures of the year. The house wren is no exception to these generalizations for other species of birds. Records show, for instance, that during the incubation period the bird may not sit on the eggs at all when the nest-box becomes excessively warm during the middle of the day. The duration of attentive periods at the nest decreases at high air temperatures. On hot days during the summer adult birds of various species are frequently seen perched with drooping wings, gaping mouths, and panting vigorously. The birds are giving the greatest possible exposure of the body in order to increase the rate of heat loss. Grimes (1931) describes how a Florida nighthawk, *Chordeiles minor chapmani* Coues, moved its eggs out of the direct sun into the shade a few inches away. Clements, in a personal note, states that western meadowlarks, *Sturnella neglecta* Audubon, and horned larks on the Great Plains seek the shade of fence posts on hot days and move with the shadow. Heat is thus a potent factor in the behavior of adult birds.

*Winter residence*—The house wren passes the winter season much farther south than where it breeds. Many passerine species have a similar difference between summer and winter ranges, while the spring and fall migrations of birds between these two regions has been much studied and the phenomenon is one of the most widely known of all biological facts. Undoubtedly, the difference in the summer and winter ranges of most birds are due to the unfavorableness of the breeding area for existence throughout the year. That a few species do survive the whole year round in particular regions from which other species migrate indicates both a difference between species in physiological adaptations and in behavior responses. Likewise, differences in migra-



tory behavior between individuals of the same species occur (Nice 1933), and this may be explained on a similar basis. In regions where all seasons of the year present optimum conditions nearly all species tend to remain stationary throughout the year. This is particularly true in the tropics (Mayr and Meise 1930).

Snow is a factor of importance for most species during the winter because it covers up and hides food, so that, deprived of food, the birds' temperature resistance decreases. Winter birds of northern regions use food not easily obscured by snow. Barrows (1889) has indicated that snow during the winter is important in limiting the abundance of English sparrows in northern localities. Birds tend to avoid these unfavorable conditions and to migrate into regions where existence is easier and more certain. Clarke (1912), who studied in great detail the numerous migration records of British and European students, gives many concrete examples to support this statement. Stantchinsky (1927), in studying the factors controlling the winter distribution of birds in eastern Europe, found that low temperature, thickness and duration of the snow covering, and food were closely linked factors. It would seem that some species migrate further south than is necessary, but this cannot be known until they are studied more intensively from the physiological point of view. Other species which ordinarily migrate south in the fall may remain in their northern habitat through at least a part of the winter if they have access to an abundant and ready source of food (Winkerwerden 1902, Hausman 1927). Their existence is hazardous, however. Shaver (1933) made an intensive study of seasonal abundance of birds in a particular habitat in Tennessee and found a correlation with the following climatic factors in approximate order of importance: temperature, sunshine duration, relative humidity, wind velocity, atmospheric pressure, and precipitation.

Many species, probably most species, migrate south only far enough to avoid average unfavorable conditions. It not infrequently happens that they do not go far enough to escape unusually severe storms and low temperatures, which frequently cause the death of thousands (Cook 1913, Forbush 1921, Rice 1924, Wayne 1899). The almost complete destruction of the eastern bluebird, *Sialia s. sialis* (Linnaeus), by low temperature and lack of food in 1895 is notable in this connection. Temperature seems to be the most important factor, especially when combined with a lack of food. Unusually cold winters may so affect the bird life that the normal abundance of species may not be regained for several years. Even the composition of the winter avifauna of a region may be changed by such occurrences (Wilson 1922). The winter of 1928-1929 in Europe was very destructive to nearly all kinds of birds, causing the death of thousands of individuals (Witherby and Jourdain 1929).

The general point to be made here is that those species of birds whose habits and physiological processes are not adapted to withstand the low temperature and other unfavorable conditions of the winter season in northern regions respond by migrating out of those regions into areas that are suited to their survival.

*Spring migration*—From the study of winter distribution of birds, it appears that those species arriving first in a region during the spring migration are those which have passed the winter nearest southward. In fact, even during the winter, warm spells may cause some birds to move about, and the singing and activity of such birds as the song sparrow and eastern cardinal, *Richmondia c. cardinalis* (Linnaeus), during these periods is well known. Apparently these species are hardier and better resist unfavorable conditions than do those which do not arrive until later in the spring, having spent the winter season further to the south.

The migration of birds appears to be attuned to the average advance of the spring as determined during preceding years. Occasionally, however, short periods of severe weather find certain species of migrating birds too far advanced. Great mortality may result, running into thousands and millions of birds (Dean 1914, 1923, Forbush 1917, 1922, Lewis 1931, Reed 1923, Roberts 1907, Smith 1929, Swenk 1922, Wood 1908). Low temperature and lack of available food are frequently the effective factors. Snow and sleet storms are thus of importance when they render food unavailable. Extremely low temperature unaccompanied by stormy weather may be better resisted than higher temperature which is accompanied by snow and ice because of the food relation. The average time and rate of migration of different species of birds are adjusted to avoid these unfavorable conditions, yet to maintain the greatest efficiency of time and reproduction. Whenever this adjustment is disturbed, fatal results occur.

The migration of birds during any spring corresponds secondarily to the prevalent temperatures of the year. When the spring temperature averages higher than usual, migration is earlier; when the temperature is lower, migration is delayed. This is borne out by the observations of several observers (Clarke 1912, Eifrig 1922, Jones 1895, 1915, 1923, Sherman 1910, Smith 1917). DeLury (1923) has attempted to correlate the time of arrival of certain European birds in the spring with the sunspot cycle. Schenk (1931) has been able to predict the time of greatest spring influx of woodcock, *Scolopax r. rusticola* Linnaeus, into Hungary by noting the position of early spring cyclonic and anti-cyclonic areas in Europe. In other instances when migration is delayed, a species may be represented in the region at about the usual time by scattered and more hardy individuals, but the main bulk of the species does not arrive until much later. As a rule, the first migrants in February and March are influenced more by temperature than are the later

ones in April and May (Brimley 1890, Kelsey 1891, Main 1932). Variations in temperature during the early spring are more effective, probably because the species are present in the adjacent regions to the south and so may reach an area to the north in one or more flights during the first favorable weather.

The migration of birds in the spring is usually not regular with a few new species dropping in day after day. Rather it occurs in "waves." Several days may go by when no new species are noted, then during a brief period of one to a few days several may come in. Ten or more such "waves" or movements may be regularly noted in the Oberlin, Ohio, region. These movements may be correlated with similar periods of warm weather occurring at the same time. The theory as to how bird "waves" are formed is that species keep moving northward until they come to a low temperature barrier where they stop. Several species and many individuals may thus become concentrated just below this barrier. Then when the barrier is lifted by a rise in temperature they all move northward at the same time. According to Stone (1891) and Smith (1917), bird waves in the spring occur only during periods of rising temperature. Cooke (1885), who studied extensively the relation of bird migration to climatic conditions, states: ". . . the greatest movement takes place on the nights of maximum heat; the next greatest on the night before the maximum; very little on the night after, and still less . . . on the minimum night of the cold wave."

The temperature of the region to the south where the birds begin their night's flight is the determining factor, not the temperature of the region northward on the date of arrival. It not infrequently happens that birds may begin to migrate under favorable conditions but before they have finished their flight enter into regions where the weather conditions are much less suitable. Cooke (1913) states: "The weather encountered en route influences migration in a subordinate way, retarding or accelerating the bird's advance by only a few days and having slight relation to the date of arrival at the nesting site. Local weather conditions on the day of arrival at any given locality are minor factors in determining the appearance of a species at that place and time. The major factors in the problem are the weather conditions to the southward, where the night's flight began, and the relation which that place and time bear to the average position of the bird under normal weather conditions." Clarke (1912) is in agreement on emphasizing this point.

From this evidence, it thus appears that birds respond to rising air temperature in the spring by returning northward to regions where they carry on their reproductive activities, and that they regulate the time and rate at which they migrate by the prevailing conditions of the environment.

*Nesting and Molting*—The temperature prevailing during the breeding season affects the behavior and activities of the birds and also the success of their reproduction. Cold, wet weather in the summer may cause con-

siderable mortality among adult and young birds during the nesting season (Clarke 1889, Cooke 1923, Forbush 1927, Hatch 1889, Purdy 1889, Saunders 1919). This is due to a direct influence of cold upon the temperature-regulating mechanism of the birds combined with an indirect influence through affecting the insect food supply. The number of birds may at times be decreased to such an extent that return to normal may not be effected for several years.

A warm spring or an early summer may hasten the time of nesting (Tollenaar 1922, Wolda 1923, Burleigh 1927, Pitt 1929, Pickwell 1931, Stevenson 1932). Wolda (1923) gives some evidence that species which begin egg-laying early in the spring vary more in time of initiating this process from one year to the next under influence of climatic factors than do those species which begin nesting much later. Birds nesting in holes or boxes begin egg-laying earlier in the spring than others, probably because of the greater protection of their nest-site. In his study of the establishment of bird territories in the spring, Howard (1929) found that temperature was a potent factor. Winter groups broke up during warm weather as individual males scattered to set up territories but reassembled during cold weather. Quail coveys behave in a similar manner (Stoddard 1931).

Porter (1908) found that after an unusually cold and late spring, most birds commenced nest-building about the average normal date, but a much longer time than normal was required to complete it, so that deposition of eggs was about two weeks late. The egg-laying period likewise extended over two or three times the normal length, and then the birds did not start incubating at once. Wolda (1923) states that there is an interruption in the beginning of nesting with sudden drops in temperature. Tinberger (1931) claims that European herons will even forsake their nests and eggs in the spring if unusually cold weather occurs.

The selection of a nest site by the adult birds may be determined in part by the necessity of protecting the young from the hot rays of the sun. It is easier for the adult birds to keep their offspring warm in the nest than it is to keep them cool, if exposed to the sun. As a consequence, most nests of passerine species are built in partial or complete shade.

The nest construction in many species is very well adapted for conserving heat when the brooding bird is absent and for applying it most efficiently when she is present. Many of the water birds, for instance, line their nests with abundant down. This they pull over the eggs at leaving. Perhaps this serves for concealment, but at the same time it is very efficient in preventing the eggs from cooling too rapidly, or in the case of such exposed nests as those of the pied-billed grebe, *Podilymbus p. podiceps* (Linnaeus), it may protect the eggs from over-heating by the sun. Woodpeckers and certain passerine species nest in hollows or holes in trees. This is true with the house



wren. Some passerine species, as typified particularly by the English sparrow and the eastern house wren, line their nest cavities with chicken feathers. Feathers make a fine insulation against cold air and retain the heat applied by the parent.

The reason why different species of birds lay different numbers of eggs per set is not clear. The statement is frequently made, however, that birds in temperate regions lay more eggs than their representatives in the tropics (Allen 1928, Fronda 1928, Rensch 1931, Averill 1933). Perhaps the environmental temperature and the general metabolism of the body may affect the average number of eggs laid. It is certainly true, that the house wren lays one or two more eggs in the first set, during the cool latter part of May, than it does in the second, during the hot early part of July.

Many theories have been formulated as to the determining factors for the length of the incubation period. No satisfactory explanation has been, as yet, given. Temperature is probably one factor involved. It is rather generally known, in the case of incubating eggs of the domestic fowl, that a higher temperature will hatch the young in quicker time than a lower temperature. The habit of incubation and complicated nesting behavior may have evolved in birds because of the advantage of hastening development by maintaining the embryos at a high and fairly uniform temperature irrespective of the temperature of the environment. This would allow more young to be raised in a season, which would be advantageous to the species. It would also permit the extension of the breeding area further northward where the temperature is not so high and where the season is shorter.

The young birds are usually divided into two groups dependent upon their physiological condition at hatching. Edwards (1839) early recognized the significance of this division. Precocial young are hatched in a relatively advanced state of development. They are covered with down, their eyes are open, and they are able almost immediately to run around and follow their parents after food. The duck and sandpiper tribes afford excellent examples. The temperature-regulating mechanism of these young birds is functional at birth, and so a semi-independent existence is possible. In contrast to this are the altricial young, as represented by passerine species. These birds are born naked, blind and helpless, and a semi-independent existence is not possible, at least until the temperature-regulating mechanism becomes functional, which is not in the house wren, until nine days after hatching. This difference in the condition of the young at birth is reflected in behavior of the adult birds and is largely responsible for it. The young ducklings follow their parents around and help obtain their own food. They are not tied to any nest site but spend the night wherever they may be. The parent birds have not developed a complex nesting behavior. Likewise, not so elaborate a nest is built, since it is forsaken as soon as the eggs hatch.

In the house wren species, an elaborate nest is built, not only to care for the eggs but also to protect the young after hatching. The young are confined to the nest and must be protected from low and high air temperature. A complex nesting behavior is developed usually involving both adult birds. The young are brooded regularly, much as the eggs were incubated, for at least ten days, or until the young develop their own temperature regulation. The young must, of course, be fed in the nest by the parents and the nest must be cleansed regularly. Usually the female broods the young every night, but sometimes when the nestlings become further developed towards the end of nest life they may be left to themselves. The young birds will live several hours at low temperature but they become inactive and cease to develop when their body temperatures drop. However, if again warmed to their normal temperature they will continue their development at the usual rate (Baldwin and Kendeigh 1932). This ability to resist for several hours a considerable decrease in their body temperature is often of value should the adult bird be detained from caring for them.

In altricial species, the young must sometimes also be protected from the sun's rays. This is particularly true of eastern kingbirds, *Tyrannus tyrannus* (Linnaeus); robins (Hancock 1911); and also European skylarks, *Alauda a. arvensis* Linnaeus (Willford 1925). This is usually done by the adult bird standing over at the side of the young and shading them with her outstretched wings. Students visiting nesting colonies of seabirds are careful not to keep the adult birds away from their young for more than a few minutes at a time on hot days or otherwise the mortality rate may be high. Excessive heat is frequently more dangerous than cold to the successful rearing of young birds.

Nestling birds are able to adjust their own behavior to some extent in order to better withstand low or high air temperatures. When the air temperature is low, young house wrens ordinarily bunch together so as to lie on top of each other. When the adult bird is away on an inattentive period, the young birds on the outside of this huddle become cool faster than those in the middle, because they are more exposed. Before the adult bird returns, the birds on the outside may become 2° to 3°F. (1.1° to 1.6°C.) cooler than those in the middle. However, this huddling together helps to maintain the temperature of all the young much better than if they were all separated. When the female returns and broods, the birds on the outside receive more heat than those within so that they soon become as warm as those which are in the middle or underneath the huddle (Baldwin and Kendeigh 1932). According to Hancock (1911), nestling wood pewees, *Myiochanes virens* (Linnaeus), and cedar waxwings, *Bombycilla cedrorum* Vieillot, during very warm weather take up positions in the nest widely apart so as best to favor the maximum radiation and loss of heat from their bodies. As the adult

birds, themselves, cannot withstand a high air temperature for great lengths of time, there is a limit to the amount of protection any one adult bird can give to its young.

The above discussion gives one an idea, at least, as to the importance of the temperature factor during the actual nesting life of birds and explains to some degree the cause for much of the bird's behavior at this time. Because of this behavior, the growth of the embryo and the nestling is practically independent of fluctuations or extremes in environmental factors.

All adult birds pass through a more or less complete molt in the late summer or fall. For many birds molting largely takes place between July and the last part of September. This is the hottest part of the year. It is of interest that molting occurs at this time when the feathers are least needed by birds to conserve heat. Also it is significant that the old, broken, worn, and lost feathers are renewed before the onset of cold weather to prepare the birds for the rigors of the winter season.

*Autumn migration*—The autumn migration of birds is affected by temperature and weather conditions much as it is in the spring except that increasing cold rather than increasing warmth induces the birds to migrate. Jones (1914) states from a study of autumn conditions that "the natural conclusion is that an early storm of snow accompanied with cold, drives the smaller migratory birds south, but does not seem to affect much the larger birds which are inclined to tarry until the lakes and streams are ice-bound." The larger water birds have a much greater resistance against low temperature than do the smaller passerine species, and usually the last individuals do not leave for the south until forced to do so by the freezing of lakes and rivers (Cahn 1912, Jung 1924). Advancing cold weather may, however, give them warning ahead of time so that they leave while there is still plenty of open water (Rowan 1929).

As the smaller birds frequently do not leave soon enough they are caught by storms and cold, with great mortality resulting (Saunders 1907). Occasionally, the larger water birds are also caught in a freeze-up, with the same results (Phillips and Lincoln 1930, p. 183). According to Brewster (1886), the smaller birds usually select clear nights for their perilous journeys southward and they start soon after dark. It is equally clear that they cannot foresee sudden changes of weather.

Thus, the life-history behavior of the house wren and other species of birds is governed partly by the physiological potentialities of the birds themselves and partly by the environmental conditions which they are forced to meet. The physiology of the bird furnishes the first basis in determining its behavior, then with this equipment it adjusts its behavior to best withstand and take advantage of the conditions of the environment. This adjustment determines the seasonal occurrence, abundance, and distribution of the species.

The next concern in this study is to determine how this adjustment affects the distribution of the species.

#### RELATION TO DISTRIBUTION

Certain conditions of climate and habitat frequently occur in regions where the combination of physiological potentialities and behavior adjustments of certain species do not permit toleration. These conditions constitute limiting factors for the distribution of the species. Were it not for limiting factors of some sort all species of animals would be uniformly distributed everywhere.

*Northward distribution*—A study was made to determine whether the critical factors of average night temperature and hours of darkness determined by physiological experiment are of actual importance in limiting in nature the northward distribution of the eastern house wren. Climatic data were compiled for the years 1921 to 1929 inclusive for twelve uniformly and widely separated localities in the optimum breeding range and for five such localities in the optimum wintering range (Fig. 1). The optimum breeding and wintering ranges include all the area over which the house wren is uniformly common or abundant during the summer or winter. Regions where the bird is uncommon or rare have, supposedly, certain unfavorable conditions of one sort or another. The climate, presumably optimum, in which the species is most abundant is considered first and then the limiting rôle of the various environmental factors in the regions where the bird is less common or absent altogether is analyzed. The climatic data were obtained from the *Monthly Weather Review*, issued by the Weather Bureau, U. S. Department of Agriculture, and from the *Smithsonian Meteorological Tables*, published by the Smithsonian Institute, 1918.

The total number of hours of darkness for all months of the year at all localities considered was computed by subtracting the total number of hours of possible sunshine from twenty-four. The number of hours of possible sunshine was determined by the method described beyond in the section on Solar Radiation (p. 375) and does not need to be described in detail here.

The method of obtaining the average night temperature needs special attention. In the *Monthly Weather Review*, only the daily maximum, daily minimum, and daily mean temperatures are given. The daily mean is the average of the daily maximum and minimum temperatures. According to Milham (1923, p. 85), the actual air temperature corresponding to the daily mean comes normally at 8:00 p.m. A verification of this is furnished by our own data showing the average of 75 days record of air temperature (Fig. 4). The average of the maximum temperature (79.0°F., 26.1°C.) and minimum (64.0°F., 17.8°C.) is 71.5°F. (22.0°C.). The air temperature at 8:00 p.m. is 71.2°F. (21.8°C.). During the summer, the birds normally cease their daily activities and settle down on their nests or roosts between 7:30 p.m.



and 8:00 p.m., so that the air temperature at this time is that of the beginning of the night, as far as the birds are concerned. During the hours of darkness at night, the temperature of the air drops more or less gradually. This drop tends to be a little more rapid in the early part of the night than after midnight (Fig. 4) but does not deviate greatly from a steady uniform depression of temperature, as would be indicated by a straight line. The daily minimum temperature is reached just before sunrise (5:00 a.m. in Fig. 4). It is at this time that darkness disappears and the birds begin their morning activities. Therefore, if the daily mean temperature comes at 8:00 p.m., when the birds settle down for the night, and the minimum temperature comes just before sunrise, when the birds begin their morning activities, an average of the two would represent the approximate average night temperature in so far as it affects the birds. These time relations may not hold closely for all latitudes and for all seasons. In winter there are several more hours of darkness than in summer, and the mean temperature of the air may not be reached at the approximate time of dusk as in the summer but at some little time after darkness has begun. The reason for this is that the temperature does not get so high during the daylight hours and continues to drop for a longer time during the night. However, the daily minimum temperature is still not attained until just before daybreak. The average night temperature may not be as accurately obtained by averaging the daily mean temperature and the daily minimum temperature in the winter as it is in the summer, but the error is not so great that the method cannot be utilized.

In order to analyze simultaneously the effect of two interacting environmental factors upon the bird in nature, use was made of *climographs*. Ball (1910) appears to have been the first to make use of diagrams of this sort for analyzing the rôle of environmental factors. Later, Taylor (1914) applied the name "climographs" to diagrams using the mean monthly wet-bulb temperature and humidity. Shelford (1929) explains the various ways of using such climatic diagrams. The term "climograph," as here used, includes all graphs or diagrams where the simultaneous effect of two climatic factors upon an organism is analyzed regardless of the nature of these climatic factors. It is permissible, therefore, to speak of a climograph when reference is to night temperature and hours of darkness. For the benefit of those who may not be familiar with the use of climographs, a full explanation and illustration is given of the summer climograph for the eastern house wren in its optimum breeding area (Fig. 13).

In considering the limiting influence of average night temperature and hours of darkness on the northward distribution of the species, it appears, first, that the species decreases in abundance before it finally disappears altogether (Fig. 1). The bird is uncommon or rare over a large part of New England, particularly Maine, while Quebec and southern New Brunswick are

as far north as it has ever been recorded. Portland, Me., and Quebec, Que., may be taken, therefore, as representative northern localities where the bird is found only irregularly or rarely. In Figure 14, the march of temperature and hours of darkness at these localities during the breeding season is compared with the climographs for the optimum breeding area. These are all averages for the years 1921 to 1929 inclusive. At Portland and Quebec the

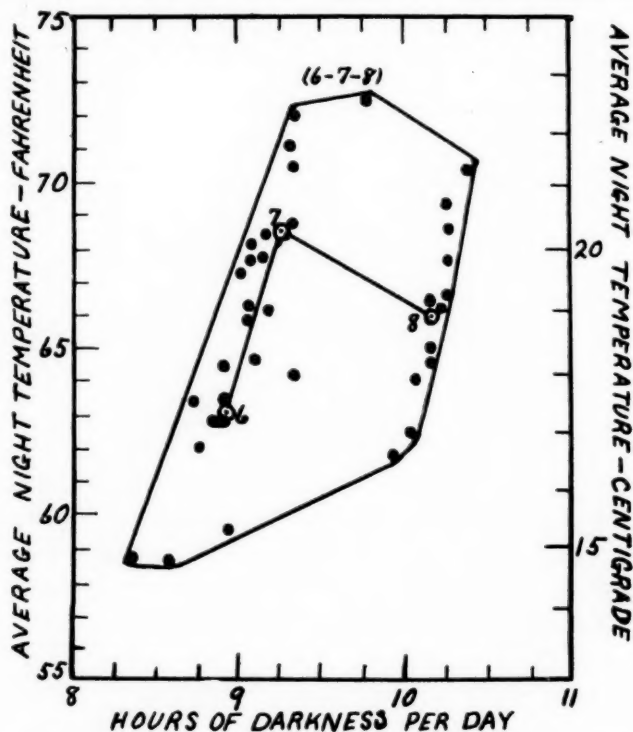


FIG. 13. Climograph for the breeding season (June, July, August) of the eastern house wren in its optimum breeding area; illustrating methods of plotting. Each dot represents the point of intersection for one month at one locality of the average night temperature and the average daily number of hours of darkness prevalent there. The climograph is drawn, after all the dots have been plotted, by running a line just outside the outermost points. The climograph then encloses an area which represents all the combinations of these two factors to which the house wren is subjected. The house wren is not subjected to combinations of these factors lying outside the climograph; usually such combinations lying outside the climograph but to the left or above may be even more favorable for the species than those to which the bird is actually subjected. The climograph thus constitutes a graphic method of analyzing simultaneously the effect of two environmental factors on a species as expressed by its distribution or occurrence in nature. The line within the climograph represents the average monthly march at all localities in the optimum breeding range, the months being indicated by appropriate numbers.

month of June (6) does not fall within the climograph at either locality. July (7) falls within the summer climograph at Portland and is favorable at Quebec as far as number of hours of darkness is concerned, but it is nevertheless low in temperature at both localities. August (8) falls outside the climograph at Quebec. This graph illustrates the unfavorableness of the

climate in these two localities for the maximum density of the species although the environmental conditions are not so extreme as to be entirely prohibitive for the presence of the species. It may well be that the abundance of the bird in this region is a fluctuating one, being more abundant during favorable warm years and less abundant during cold years. The house wren

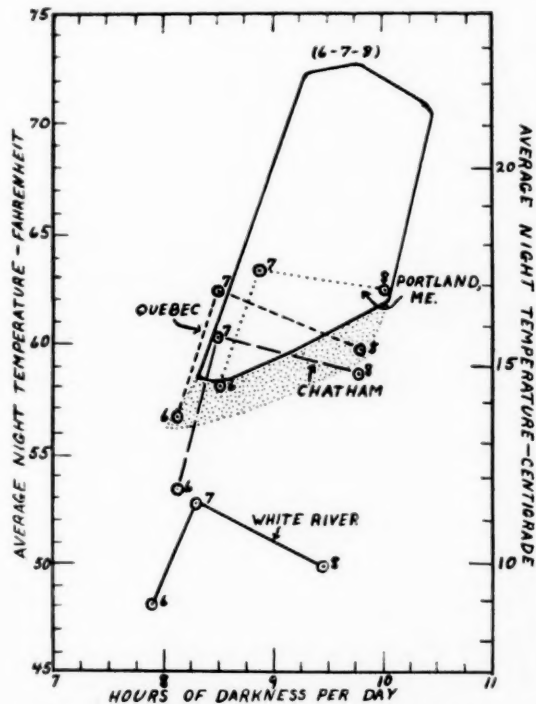


FIG. 14. Climograph for the breeding season (months 6-7-8) of the eastern house wren together with the monthly march of average night temperature and hours of darkness daily at Portland, Me., and Quebec, Que., where the species is uncommon, and Chatham, N. B., and White River, Ont., where it is absent entirely. The stippled area is an intermediate zone between distinctly favorable and distinctly unfavorable climatic conditions.

is rarer at Quebec than at Portland. Apparently climatic conditions at Quebec are close to the limit of tolerance of even the most hardy individuals.

Chatham, N. B., lies just north and outside of the breeding range. Comparing the monthly march there (Fig. 14) with Quebec, it is seen that while the number of hours darkness averages the same the night temperatures are

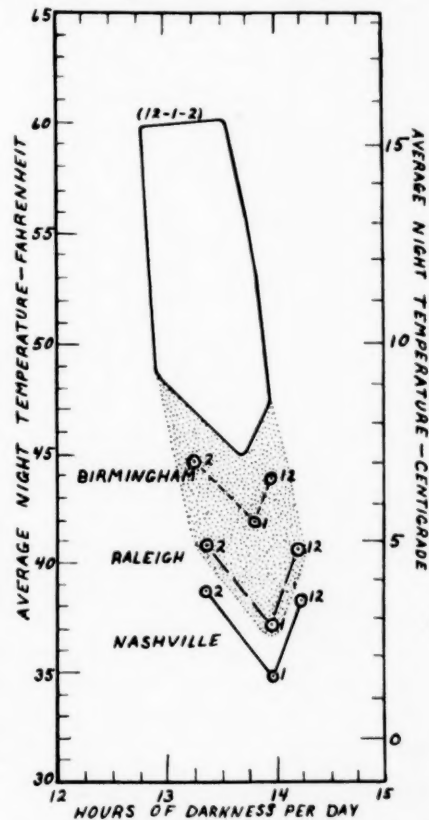


FIG. 15. Climograph for the wintering season (months 12-1-2) of the eastern house wren together with the monthly march of average night temperature and hours of darkness daily at Birmingham, Ala., and Raleigh, N. C., where the species is uncommon, and at Nashville, Tenn., where it is entirely absent at this season. The stippled area is an intermediate zone between distinctly favorable and distinctly unfavorable climatic conditions.

lower and are apparently beyond favorable limits. At White River, Ontario, the temperatures are still lower, although the nights are shorter. With monthly mean temperatures, so low, during many nights the temperature must approach the limits of toleration. Compare with Figure 12. A study of these data in relation to the distribution of the species verifies the importance of night temperature and hours of darkness as limiting factors in the northward distribution of this species. As one goes northward, night temperatures, even during the summer, become increasingly lower and unfavorable. The fact that the daily period of darkness also becomes shorter northward in the summer compensates to some degree for the drop in temperature, although not sufficiently to prevent the bird from reaching a climatic barrier to its spread. If the birds were unencumbered with nesting duties and the consequent utilization of energy for reproduction they might occur further north than they do.

The question arises next as to how universally these factors may be applicable for limiting the northward distribution of all birds. The only comparison that can be made at this time is with the English sparrow. At approximately 32°F. (0.0°C.) the resistance time of the house wren is 9.9 hours in the early part of the summer, while that of the English sparrow is 17.9 hours. The greater resistance time of the English sparrow is correlated with the fact that it extends farther north into Canada than does the house wren.

The northward distribution of the house wren during the winter is affected by number of hours darkness and average night temperature in a similar manner as during the summer. As the house wren is able to increase its resistance to a certain extent in winter over what it is in the summer, it is able to tolerate somewhat lower night temperatures and a larger number of hours of darkness, as indicated in Figure 15. There are, however, limits to the extent to which it can do this. At Birmingham, Ala., and Raleigh, N. C., the nights are too long and the temperatures are too low during the winter months to be readily tolerated by the majority of the individuals of the species. Only the few most hardy individuals occur here. At Nashville, Tenn., night temperatures drop even lower and the bird is not known to winter either here or farther north. The width of the intermediate zones in Figure 14 and Figure 15 may indicate that low temperature in the winter is less exacting in its limiting rôle upon distribution than it is during the breeding season, probably because no energy is lost during the winter months on the duties of reproduction and all of it may be conserved for self-maintenance.

In view of the data presented in Tables 6 and 7 it would seem probable that only the heaviest, largest, and most resistant individuals of any species would be found along the northern boundary of the bird's range. The work of some of the earlier ornithologists substantiates this idea. Baird (1866)



TABLE 19—Increase in temperature southward, averages for 1921 to 1929 inclusive, and effect upon presence of eastern house wren in region. For location of places, see diagram, Fig. 1.

Locality	Presence of bird	JUNE				JULY				AUGUST				AVERAGE			
		Mean daily maximum		Absolute maximum		Mean daily maximum		Absolute maximum		Mean daily maximum		Absolute maximum		Mean daily maximum		Absolute maximum	
		°F.	°C.	°F.	°C.	°F.	°C.	°F.	°C.	°F.	°C.	°F.	°C.	°F.	°C.	°F.	°C.
Optimum breeding area.	Common to abundant	77.4	25.2	91.1	32.8	82.2	27.9	93.0	33.9	79.8	26.6	90.8	32.7	79.8	26.6	91.6	33.1
Indianapolis, Ind.	common	80.4	26.9	92.8	33.8	85.1	29.5	94.1	34.5	82.6	28.1	92.2	33.4	82.7	28.2	93.0	33.9
Washington, D. C.	common	82.4	28.0	94.7	34.8	85.6	29.8	97.0	36.1	83.1	28.4	94.9	34.9	83.7	28.7	95.5	35.3
Richmond, Va.	common	83.8	28.8	95.0	35.0	87.2	30.7	96.3	35.7	84.8	29.3	96.0	35.6	85.2	29.6	95.8	35.4
Louisville, Ky.	uncommon	82.7	28.2	92.7	33.7	87.1	30.6	95.7	35.4	84.0	28.9	94.6	34.8	84.4	29.1	94.3	34.6
Raleigh, N. C.	absent	85.2	29.6	96.0	35.6	87.6	30.9	95.6	35.3	85.9	29.9	94.9	34.9	86.2	30.1	95.5	35.3
Nashville, Tenn.	absent	85.0	29.4	93.6	34.2	88.8	31.6	96.1	35.6	88.6	31.4	94.7	34.8	87.5	30.8	94.8	34.9
Birmingham, Ala.	absent	87.8	31.0	95.4	35.2	90.0	32.2	96.8	36.0	90.4	32.4	98.0	36.7	89.4	31.9	96.7	36.0
Optimum wintering area.	absent	88.2	31.2	95.2	35.1	89.3	31.8	95.7	36.0	89.6	32.0	95.3	35.2	89.0	31.7	95.4	35.2

proposed a law as follows: "North American birds of wide distribution in latitude, whether migrant, or residents, will be found to be larger the higher the latitude of their place of birth." Allen (1871) accepted and gave additional proof of Baird's law that birds, and also mammals, decrease in size at lower latitudes and altitudes, and stated that this decrease in size may amount to as much as 12% to 20%. European scientists have likewise recognized this decrease in size of birds southward (Rensch 1931) and dignify the phenomenon as "Bergmann'sche Regel."

*Southward distribution*—In considering temperature as a factor limiting the southward distribution of birds, the daily maximum temperature is most important as it represents the daily extreme of heat to which the birds are subjected and to which they must first become adjusted if they are to remain in the area. The maximum temperature should not reach such a point that the metabolism of the bird becomes too greatly reduced for normal activity to be carried on, nor should the maximum temperature remain long above the upper critical temperature (93.0°F., 33.9°C.).

In Table 19 the increase in temperature southward is indicated and the presence or absence of the house wren noted. The averages of mean daily maximum and absolute maximum temperatures for the three hottest summer months are lowest in the optimum breeding area. Indianapolis, Washington, and Richmond are near the southern boundary of this area. Temperatures are higher here than the averages for the optimum breeding area as a whole, but not so high that they are intolerable for the house wren. At Louisville, Ky., the temperatures are about the same or lower than at Richmond. The species occurs at Louisville but is uncommon, while at Richmond it is common. The difference in temperature does not account for the difference in the abundance of the bird in these two localities. It would seem that some other factor enters in here, and this will be shown later to be true (p. 391). From Raleigh, N. C., and Nashville, Tenn., southward, the house wren is absent during the breeding season. This corresponds with an increase of the daily mean maximum temperature above 86°F. (30.0°C.). In the wintering area of the species the mean maximum during the summer is 89.0°F. (31.7°C.). With the mean maximum temperatures so high, on many days the temperature must rise above the upper critical temperature of 93°F. (33.9°C.). Obviously, these high temperatures are unfavorable for the carrying on of normal activities by the birds and explain, in large measure, their absence. It appears from Table 19 that absolute monthly maximum temperatures do not have as great an importance in limiting the southward distribution of this species. The reason for this probably lies in the fact that such high temperatures ordinarily occur but once each month and are maintained for only a few hours and that such occasional temperatures may be almost as high in the north as in the south. The birds are able to survive

several hours of such temperatures by remaining comparatively inactive or seeking the coolness of shrubs or woods. The mean maximum temperature is of more significance because it represents the persistent daily condition for the entire month.

Table 7 indicates that lighter birds live longer at a high air temperature than do heavier birds, except where the air temperature is extremely high. The lighter birds, on the contrary, have less resistance to low air temperature than do the heavier birds. The inference from these data is that individual birds lighter than the average should occur along the southern border of the species' range. That this is true is indicated in the work of Baird (1866), Allen (1871), and Rensch (1931) to which reference has already been made.

The southward distribution of the house wren in the wintering area is not controlled by temperature but by a physiographic feature, the Gulf of Mexico. The species goes as far south as it can on land, and is apparently most abundant in middle and southern Florida. At Tampa, Fla., the mean daily maximum temperature of the coldest month of the year, January, is 70.3°F. (21.3°C.) and the absolute maximum is 81.3°F. (27.4°C.).

The southern boundary of the breeding range of the English sparrow is of interest in this connection. The English sparrow has a greater resistance time at 100°F. (37.8°C.) than does the house wren (p. 338). This is correlated with its more southerly distribution, since it occurs during the breeding season in the Gulf States and West Indies. Swenk's work (1929) with pine siskins, *Spinus p. pinus* (Wilson), in southeastern Nebraska bears on this point. He finds that this species nests in that region when the spring temperature is below normal, but leaves the region and nests further north when the spring temperature is high.

*Eastward and westward distribution*—The breeding and wintering ranges of the house wren are bounded and limited on the east by the Atlantic ocean. Westward, there is no such physiographic barrier to distribution. It is to be recalled that a paler western form of the house wren (p. 302) extends from where the eastern form leaves off clear to the Pacific Ocean. Recent work of Landauer (1933) indicates that differences in temperature may affect the degree of pigmentation of feathers. Three stations (Lincoln, Neb., Denver, Colo., Portland, Ore.) were selected for study to determine whether temperature or any other climatic factor varied sufficiently to be significant in limiting the westward distribution of the eastern subspecies. The monthly march of average night temperature and hours of darkness during the breeding season was plotted for each of these localities. All months fall within or very close to the limits of the climograph for the optimum breeding season. The figure is not reproduced here as it was obvious that these two factors were of no importance in limiting the distribution of the eastern house wren westward. Likewise, Lincoln has a mean daily maximum temperature during the sum-

mer comparable to Richmond, Va.; Denver and Portland, Ore., both have low maximum. Some other factor than temperature is important in limiting the bird's distribution westward.

#### RELATION TO MIGRATION

The cause and regulation of the annual migration of birds north and south have been the source of wonder, mystification, and scientific theorizing for ages. As yet no adequate explanation has been offered. Temperature, as a causative and regulatory force in bird migration, has been discussed and criticized over and over again in the past. Present day writers are inclined to minimize the importance of temperature, but mostly without sufficient basis in experimental evidence or careful study of what the critical effects of temperature may be. Birds have wide limits of tolerance, as has been shown, to extreme degrees of high and low temperatures lasting for only short periods, so that such temperatures, in themselves, do not control migration; and most of the controversy has been along these lines. The attempt in this paper is to show that temperature is of prime importance when a time factor enters in, both in the case of the night temperatures and maximum temperatures.

*Autumn migration.*—In Figure 16, climographs are shown for all seasons of the year. These climographs represent all combinations of average monthly night temperature and number of hours darkness to which the eastern house wren is actually subjected in its optimum breeding and optimum wintering areas and during migration. The average monthly march is also shown for the optimum breeding area throughout the year and the optimum wintering area throughout the year. All months from October to April in the breeding range fall outside the climographs. Temperatures at night fall much too low and the nights are too long for the existence of the species. Short periods within each month with still lower temperatures than those indicated by the averages would be especially critical. The conclusion is inescapable that the breeding area of the house wren is not suitable for the existence of the species over winter and that the species must leave that area for these months if it is to maintain its existence. Some preliminary results from experiments in confining house wrens during the winter in cages out-of-doors in the north tends to confirm this conclusion.

The house wren must undergo some adjustment or acclimation in the winter to longer nights and lower temperatures even in its wintering area, but there is not nearly as much as would be required if the species were compelled to remain further north. Those house wrens which migrate into southern Florida need make very little adjustment at all, as the winter temperatures are high and the nights are not so long. The advantage of migration to the bird is, therefore, evident, since it keeps them under tolerable conditions during all seasons of the year.



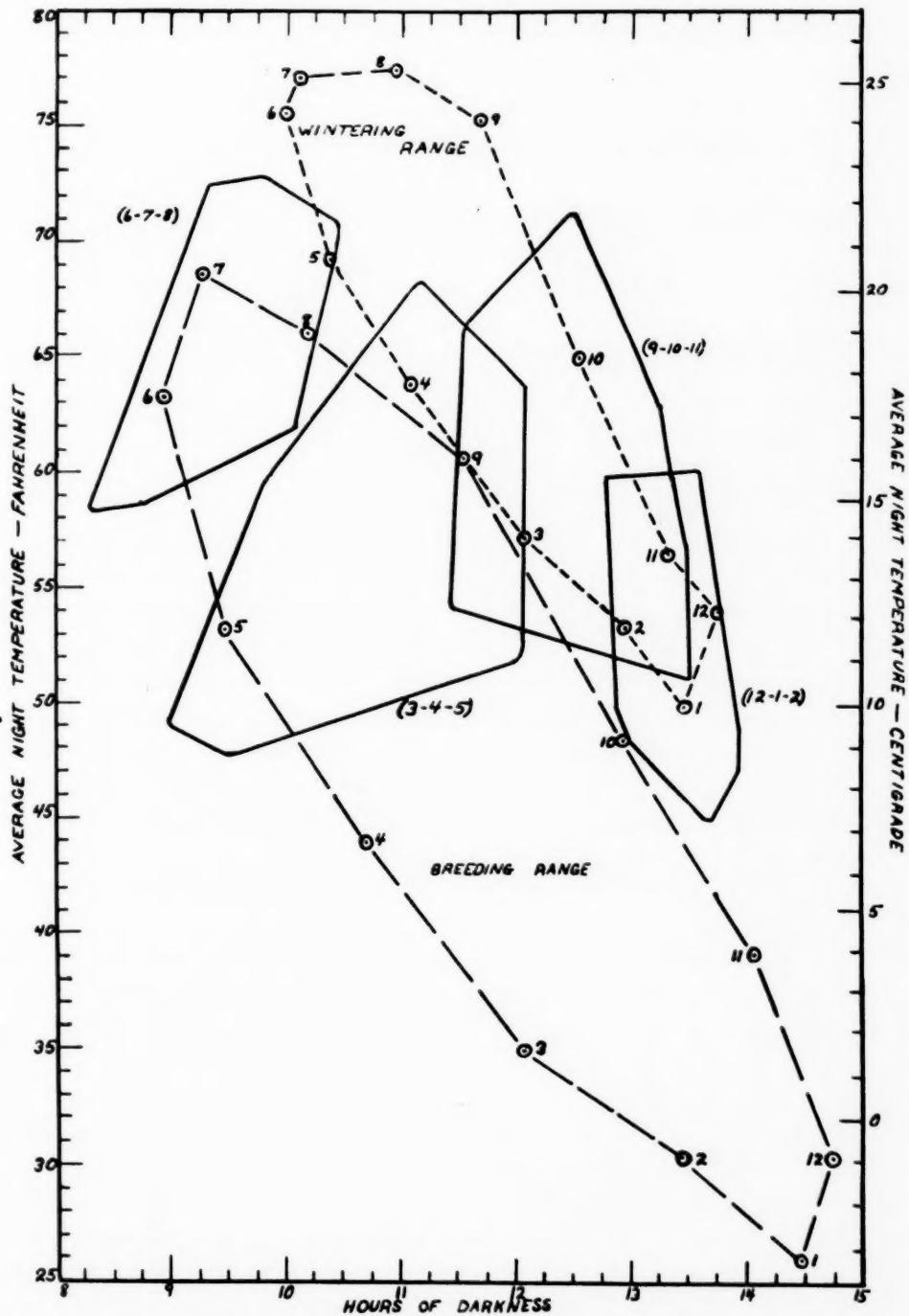


FIG. 16. Seasonal climograph showing all combinations of average monthly night temperature and hours of darkness daily to which the eastern house wren is subjected throughout the year, together with the average monthly march of these factors as they occur throughout the year in the breeding and wintering ranges.

The migration of the house wren out of the breeding range is completed by the last of September or the first of October. As shown in Figure 16, this is long before the onset of the intolerably long cold nights of midwinter. These intolerable conditions do not, therefore, determine the time when the birds begin to migrate. This is dependent upon more complicated relations. After the summer solstice of June 21st, the nights become gradually longer. Birds are sensitive and responsive to variations in day length (Allard 1930) and so are also responsive to variations in the number of hours of darkness. During July, the night temperatures are higher than in June and the period of darkness less than a half-hour longer. These combinations are all very favorable for the existence and activity of the bird. During August, however, the daily period of darkness increases more rapidly at the same time that the night temperature begins to drop, and this continues in an increasing degree during September. The climatic environment is becoming less and less favorable in a continuous although irregular and fluctuating manner. This certainly affects the bird and its behavior and may very probably serve as a warning of severer climatic conditions to come. The regulation of the time of autumn departure of the house wren during August and September may actually lie in these increasing daily periods of darkness and dropping temperatures. The birds thus leave the region before the onset of conditions which would jeopardize their existence. The time margin of safety is broad enough to prevent undue mortality, although even then occasionally early or unseasonable weather may cause distress. Other elements and factors enter into the timing of migration, so further details and discussion will be postponed until later in the paper.

*Spring migration*—As evident from Figure 16, the daily period of darkness becomes increasingly shorter and the night temperature becomes increasingly higher during the spring months in both the wintering and breeding areas. By the last of April or early May the night temperature becomes sufficiently high and the period of darkness sufficiently short to allow the return of the house wren into the breeding area.

Over most of its wintering range the house wren has been subjected to lower temperatures and longer nights than during the breeding season previous and has been compelled to regulate its metabolism, activity, and general resistance to meet these conditions. With the alleviating of these conditions with the coming of spring, there is less demand from the energy of the bird for self-maintenance, and there is a surplus available for other purposes. The release of this surplus of energy for other purposes than self maintenance may well serve as one of the factors to regulate the time of spring migration.

However, shorter nights with higher temperatures are favorable for birds, and there would be no reason for the birds to leave the wintering area in the

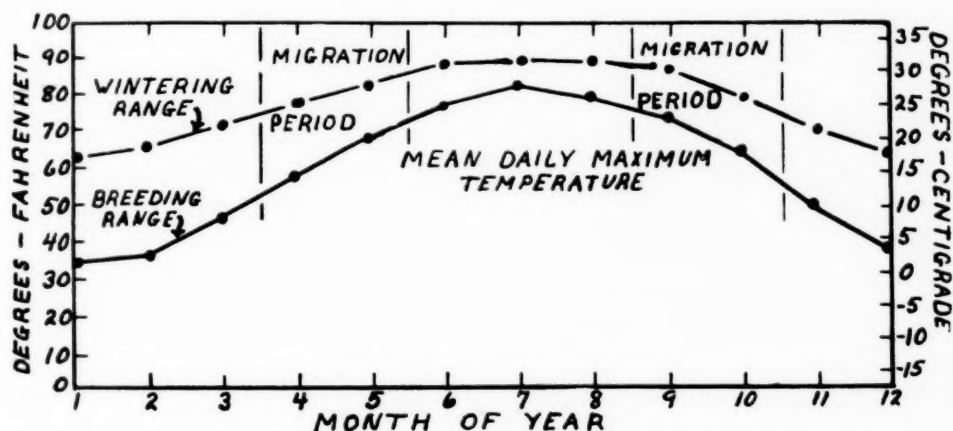


FIG. 17. Monthly variation of the maximum temperature in the breeding and wintering ranges of the eastern house wren.

spring unless one or more other factors became increasingly unfavorable at the same time. On foregoing pages data are presented indicating that the house wren is limited in its southward distribution, during the breeding season, by the high maximum temperatures reached in the summer during the daylight hours. As the days become longer in the spring, mean daily maximum temperatures become higher. The highest temperature that the house wren tolerates in its breeding range in midsummer is reached in its wintering range in May (Fig. 17). The fact should be borne in mind, also, that the resistance of the house wren to high air temperature is less in May, and presumably also during the winter, than it is in the middle of the summer. From May until October, the mean maximum temperature in the wintering area becomes excessively high. The rise in mean daily maximum temperature must be, therefore, a factor in regulating the time of northward migration. The house wren begins to leave its wintering range in late March or early April and is probably entirely out by May. There is a time margin of safety in the migration of birds in the spring as well as in the autumn, yet they cannot to advantage leave for the north before conditions become favorable for them there.

An interesting point involved here in both the spring and autumn migrations of birds, is the effect of the bird's weight upon the time at which it migrates. It was shown in Table 7 that heavier birds have a greater resistance to low air temperature than have lighter birds, while the lighter birds tolerate high air temperature for a longer time than do the heavier birds. Arguing from this, the heavier individuals of a species should arrive earlier in the spring than do the individuals of less weight; while in the autumn, the heavier individuals should be the last to go. Allen (1871) noticed that this was actually true in the case of certain Gnatidae and in *Tringa*. Likewise, Whittle (1927) found that in Massachusetts song sparrows that migrate through in April are about five grams heavier than birds remaining to

breed. A relation between bird weight and time of migration was also found true at our laboratory when a large number of white-throated sparrows, *Zonotrichia albicollis* (Gmelin), and white-crowned sparrows, *Zonotrichia l. leucophrys* (Forster), were weighed and the date analyzed. No distinction was made in the summary (Table 20) between the age and sex of the birds, as it has already been shown that the temperature resistance is apparently not influenced by these factors (p. 326).

TABLE 20—The average weight of birds during the first and second halves of their migration through Gates Mills, Ohio.

Species	Number of birds	Average weight, first half migration: grams	Number of birds	Average weight, last half migration: grams
<i>Zonotrichia albicollis</i> (Gmelin).....	16	(Spring) 29.3	8	(Spring) 28.1
<i>Zonotrichia l. leucophrys</i> (Forster).....	19	33.0	19	29.9
<i>Zonotrichia albicollis</i> (Gmelin).....	119	(Autumn) 26.4	94	(Autumn) 27.4
<i>Zonotrichia l. leucophrys</i> (Forster).....	27	28.7	21	30.6

#### RELATION TO ABUNDANCE

The eastern house wren decreases in abundance around the periphery of its breeding area before it finally disappears. The reason for this decrease lies in the approach of one or more factors towards the limits of tolerance (p. 353). The house wren likewise varies in its yearly abundance (Table 1). In considering the influence of climatic factors upon these yearly fluctuations in abundance, the amount of reproduction and the survival over winter must be studied separately.

In Figure 18, the average night temperature at Cleveland, Ohio, for the months of May, June, and July is plotted along with the curve showing relative amount of reproduction from year to year. August is omitted since new house wren nests are seldom begun during this month. Other factors of temperature vary similarly as does the night temperature, as do also averages for the breeding area as a whole. The minimum possible hours of darkness is of course the same from year to year and so does not need to be included in this discussion. A general correlation between temperature and reproduction is evident in this figure, although there is some inconsistency in detail due to the conflicting influence of other factors. There is a good physiological reason for the night temperatures to have an effect upon the amount of reproduction. When the night temperature is low, more energy must be used for self-maintenance than when the night temperature is high. This would leave less available for the carrying on of activities during the



daytime, would require more time during the day for rebuilding the resistance required for the following night, and consequently less time and energy would be available for the duties of reproduction. It thus appears that the average night temperature during the breeding season is one factor concerned in determining the amount of reproduction and abundance of the bird the following season.

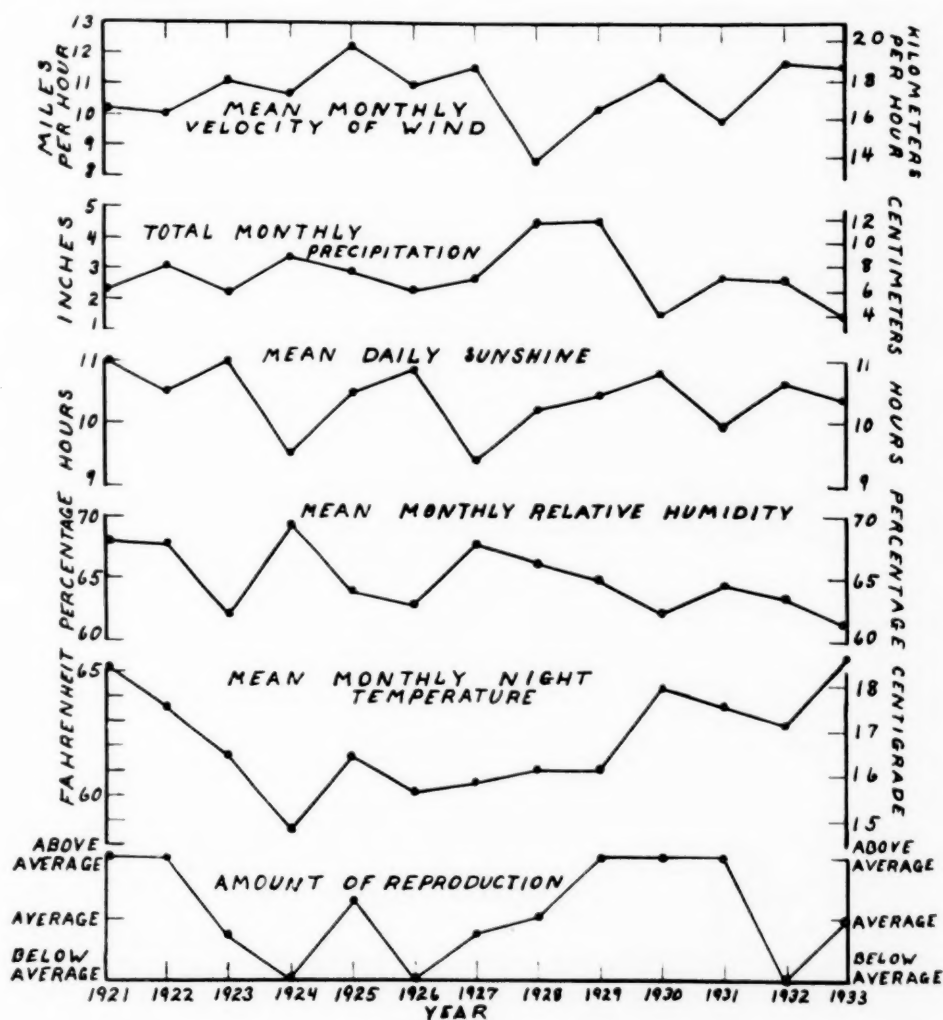


FIG. 18. Correlation between relative amount of reproduction of the eastern house wren from year to year and various climatic factors during May, June, and July at Cleveland, Ohio.

In Figure 19, the average night temperatures during the autumn (September in breeding range, October and November in wintering range), winter (December, January, February in wintering range), and spring (March and April in wintering range, May in breeding range) are shown in relation to the relative amounts of survival over the winter period. The low rate of

winter survival in 1925 and 1930 correlates with the lowest winter temperatures of any year during the whole period. Fluctuations in the average night temperature during the winter months from one year to another agree fairly well with fluctuations in the curve showing the survival rate. An average night temperature of 50°F. (10.0°C.) appears particularly critical as below this temperature great mortality resulted. The low rate of survival in 1921 does not correlate with low night temperature—apparently some other

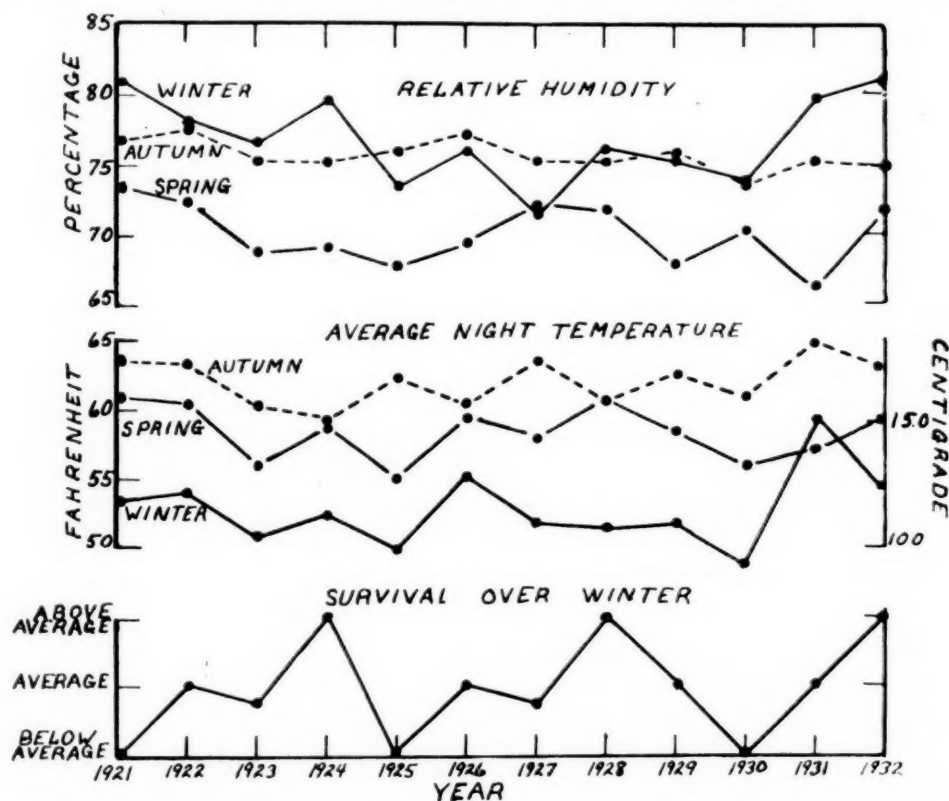


FIG. 19. Correlation between yearly variations in relative amount of survival of the eastern house wren over winter and seasonal averages of night temperature and relative humidity to which the species was subjected.

factor than temperature was important in this instance, provided the rate of winter survival was correctly determined during this, the first, year of intensive study. Spring temperatures, though higher than winter temperatures, appear even more closely correlated with survival and undoubtedly augmented or modified the effect of winter conditions. No correlation at all is possible between survival rate and autumn temperatures. Mean maximum as well as other average temperatures varied during this period much as did the night temperature, but they appear to have no particular significance.

#### IV. RELATIVE HUMIDITY

Relative humidity and temperature are closely interacting factors in nature. When temperatures rises, relative humidity usually decreases, and when temperature drops, the relative humidity rises. However, a low relative humidity may not infrequently occur with a low temperature and a high humidity with a high temperature. Unless the relative humidity has been controlled or allowed for, effects frequently ascribed to a high or low temperature in physiological experimentation are the result also of varying conditions of relative humidity.

##### PHYSIOLOGY AND BEHAVIOR RESPONSES

At low temperature a high relative humidity may be detrimental to mammals because it increases the conductive power of the air and thereby accelerates heat loss. With birds, this effect of high relative humidity at a low temperature may be significant, since rate of conduction of the air would be important in the giving off of heat on the body and in lungs and air-sacs. Low temperature, then, is probably more endurable when the relative humidity is also low than when it is high.

At a high air temperature, a high relative humidity prevents rapid evaporation of sweat and cooling of the body in the case of those mammals possessing sweat glands. Thus high temperature has a more detrimental effect upon the animal than when the relative humidity is low, in spite of its greater conductive capacity. Evaporation goes on from the walls within the air-sacs and lungs of birds, and this increases greatly in amount at high air temperature (Fig. 7). Relative humidity would supposedly have a similar effect on evaporation of moisture as with mammals. That this is true is evidenced from the limited amount of experimental work which we have performed (Table 9). In other words a high temperature is resisted better when the relative humidity is low than when it is high.

In the development of the embryo in the egg, relative humidity would act as in cold-blooded organisms. A high relative humidity would tend to conserve heat at high air temperatures by decreasing evaporation, while a low relative humidity would tend to increase its dissipation. Romanoff (1929) has found in the case of the white leghorn that a relative humidity of 80% during incubation favors a more rapid growth and calcium metabolism, but causes heavy mortality just before hatching. A relative humidity of 40%, on the other hand, retarded growth and calcium metabolism but had scarcely any effect on the mortality of the embryo. As no measurements of relative humidity in the nest of the eastern house wren have been made, the discussion cannot be carried far here. Since the nest temperature is maintained fairly constant, the relative humidity also may not vary so much as in the air generally. It is true that the eggs lose water constantly from the beginning

of incubation till hatching. A uniform relative humidity in the nest would keep this loss rather constant. Taverner (1933) has made the suggestion that purple martins, *Progne s. subis* (Linnaeus), keep their nest supplied with fresh green leaves in order to control the relative humidity favorable for incubation purposes. The behavior and attention of the adults appear to be adjusted to keep the eggs under nearly optimum conditions.

Beebe (1907) carried on experiments with doves, *Scardafella* spp., to determine the effect of relative humidity on the color and pigmentation of the bird's feathers. He confined them in a super-humid atmosphere and found that a radical change in the pigmentation of the plumage took place with each succeeding annual molt. In general, there was an intensification of the melanin and later a spread into surrounding parts of the feather so that all trace of white disappeared. These experiments are not well described and not certainly due to the effect of relative humidity alone. However, they agree with the general observation frequently made that among closely related forms, those occurring in the humid tropics tend to have darker plumage than those in arid regions, which commonly have light tans, browns, and grays (Allen 1871, Rensch 1931).

TABLE 21—Average relative humidity (percent.) during June, July, and August both within and without the optimum breeding area of the eastern house wren.

Locality	June	July	August	Average
Optimum breeding area.....	68.9	71.6	72.6	71.0
Indianapolis, Indiana.....	66.6	64.0	69.0	66.5
Grand Rapids, Michigan.....	63.6	61.9	67.2	64.2
Lincoln, Nebraska.....	61.2	65.8	64.6	63.9
Denver, Colorado.....	52.1	52.4	53.2	52.6
Portland, Oregon.....	65.9	62.1	65.1	64.4

#### RELATION TO DISTRIBUTION

A careful use of the climographs was made to determine if relative humidity could be limiting in any way on northward and southward distribution, but no such direct effect could be found, although the wintering area has generally a higher relative humidity than the breeding area (Table 22). Westwardly, the eastern house wren, *T. a. acdon*, is replaced by the western house wren, *T. a. parkmani*. Since the difference between the two subspecies lies principally in the somewhat grayer plumage of the latter, the transition between the two types is probably a gradual one. Table 21 shows that the relative humidity decreases westwardly until it becomes very low at Denver, although at Portland, Ore., it is again higher. From this, it appears that a lowering of relative humidity may be in some way concerned in the change of the coloration that occurs between these two subspecies.



## RELATION TO MIGRATION

In Table 22, the relative humidity in the breeding and wintering areas is compared for all months of the year, based on averages for the years 1921 to 1929 inclusive. The relative humidity is higher during every month in the wintering area than it is in the breeding range. From June to September, this may have some importance, since the relative humidity is then combined with very high temperature (Fig. 17).

TABLE 22—Average monthly relative humidity (percent.) throughout the year in the optimum breeding and wintering areas of the eastern house wren.

Month	Optimum breeding area (exclusive of Canada)	Optimum wintering area	Area in which bird is present
January.....	74.0	76.0	wintering
February.....	75.6	76.2	wintering
March.....	70.6	73.6	wintering
April.....	65.3	72.5	migrating
May.....	66.4	73.1	migrating
June.....	68.9	77.7	breeding
July.....	71.6	79.5	breeding
August.....	72.6	80.1	breeding
September.....	75.7	80.0	migrating
October.....	74.1	76.3	migrating
November.....	74.0	77.4	wintering
December.....	75.4	77.3	wintering

## RELATION TO ABUNDANCE

In Figure 18 the average relative humidity during the three breeding months of May, June, and July is plotted for comparison with the relative amount of reproduction from year to year. Apparently no correlation exists between the two, either separately or in conjunction with temperature.

The average relative humidity during the autumn (September in breeding range, October and November in wintering range), winter (all months in wintering range), and spring (March and April in wintering range, May is breeding range) has been plotted in Figure 19 for comparison each year with the survival rate over winter. The curves for the autumn and spring show no correlation with amount of survival, but the curve of average relative humidity for the winter is positively correlated in its fluctuations with survival rate and, to a lesser extent, with temperature, except during 1921. The significance of the positive correlation is unknown, since, on the basis of present physiological knowledge, relative humidity should be correlated inversely with low temperature to be effective on survival. Likewise, simultaneous and similar variations in relative humidity and high temperatures might reasonably be correlated inversely with survival rate, rather than positively as it is here. Further study of the rôle of relative humidity affecting birds is required.

## V. SOLAR RADIATION

Solar radiation is important in the lives of birds because of its daily duration, its intensity, and its wave-length composition. These points will be discussed briefly.

## PHYSIOLOGY AND BEHAVIOR RESPONSES

There is a daily rhythm in bird activities and in their physiological responses which is dependent upon the relative lengths of day and night. The daily rhythm in body temperature has already been considered (Fig. 4). In addition, there is a corresponding variation in metabolism and in the activity of many of the body tissues. There is ordinarily a depression in the body functions of diurnal birds at night, which makes the relative duration of this period of lowered activity important in the general physiology of the bird. During the longer days, more work, of course, can be accomplished and more energy will be utilized. Rörig (1905) and Groebbels (1931) found that certain caged birds consumed a larger amount of food per day in the summer than in the winter, which they explain on the basis of a longer daylight period.

Different species of birds have somewhat different daily periods of activity due to the difference in their responses to the varying intensities of light in morning and evening (Wright 1912, 1913, Allard 1930, Shaver and Walker 1931). Some species respond to lower intensities of light in the early morning in late June than at other seasons of the year (Allard 1930). Drost (1931) suggests that the time at which migrating birds begin and end their daily flights may be correlated with the intensity of sunlight in the evening and morning. Lutz (1931) found in a species of house wren, *Troglodytes musculus inquietus* (Baird), in Panama that an individual bird during twenty-four mornings began to sing at nearly the same time. If the morning was unusually bright the first song came a little early, if cloudy, it came later, but never varied more than fifteen minutes. With the eastern house wren the male, during the nesting season, becomes active fifteen to thirty minutes before the female. The reason for this is that he roosts in shrubbery or vines where he is sooner affected by the break of day than is the female who stays all night in the dark nest-box. Owls and some other species are more active at night, and obtain their rest during the daylight hours.

The striking effect which an increased day-length has upon an increased reproductive ability of birds is well illustrated in the case of the domestic fowl. According to Kennard and Chamberlain (1931): "A restricted amount of artificial light has long been used to advantage for increased egg production. All-night light is a more recent development and extension of the same principle. The evidence presented would seem to indicate that all-night light is the most effective way to realize fully the value of artificial light for winter

layers. The supposed ill effects from the unrestricted use of light failed to materialize."

Rowan (1929) found, in the case of slate-colored juncos and later in American crows (1931) kept in captivity, that by artificially increasing the daily period of light the bird's gonads were caused to increase remarkably in size, and that by diminishing the daily period of light the gonads decreased in size. He believes this effect of length of day on the gonads was produced indirectly through regulation of the daily amount of the bird's activity. Bissonnette (1932), working with starlings, and Cole (1932), working with mourning doves, have verified Rowan's results on the controlling influence of length of day for regulating the size and functioning of the gonads. Bissonnette does not believe, however, that this influence is exerted indirectly by the modification of the amount of the bird's activities, but believes that the solar radiation acts directly through some effect on the bird itself. Time has not yet permitted a complete analysis of all the possible intermediate factors. Cole (1933) suggested that species or geographical groups of individuals may vary genetically in their gonadal response to length of day, some birds requiring longer or shorter days for the gonads to mature. He further suggested that if this is true birds would presumably be limited in their northward and southward distribution to the latitudes with proper daily proportions of light and darkness. That length of day is not the only factor involved in determining the time of gonad activity is shown by recent studies of Bissonnette (1932), Davis (1933), Lack (1933), and Linsdale (1933). Special studies still need to be performed on tropical birds to determine the manner in which the gonads are stimulated to develop where day and night are of nearly equal duration throughout the year.

Rowan (1929, 1931) attempts to correlate length of day, development of gonads, and bird migration. Some evidence is furnished that certain hormone-secreting interstitial tissues in the gonads are present only when the gonads are increasing and decreasing in size, but not when they are at their maximum and minimum size. When juncos whose gonads were increasing or decreasing in size were liberated, he found that many disappeared, while those whose gonads were not changing in size mostly stayed near the point of release. Under natural conditions, most birds do migrate north in the spring when their gonads are increasing in size and migrate south when they are diminishing in size. Rowan thus believed that the stimulus for these migrations was furnished by hormone secretion from the gonads in spring and fall. One wonders, however, if this interstitial tissue may not also be present in the gonads of permanent resident species which do not migrate but whose gonads likewise undergo remarkable seasonal changes in size. If the influence of temperature and other environmental factors in regulating the time, manner, and extent of migration is ignored in favor of the gonad theory, how will

the many obvious correlations between the distribution, migration, and abundance of birds and environmental conditions be explained? In later work with the American crow, where the wanderings of marked experimental birds could be followed with greater exactness, Rowan (1932) has been unable, as yet, to get decisive proof for the controlling influence of gonads in migration. Birds that had been castrated or treated in other ways, as well as the untreated controls, all migrated southward in a similar manner after liberation in late autumn, indicating as Rowan himself states, that southward migration, at least, is independent of the influence of the gonads. Because of these difficulties the theory that a hormone from the gonad is the only or even the chief stimulating and controlling agent in bird migration cannot be accepted. It may be one factor or influence involved—along with other endocrine glands, with the general physiological state of the bird, and with the action of the environment. It seems that if the gonads are to affect migration it must be through some influence on the physiological state of the bird which is, at the same time, under influence from various other sources as well.

Schaefer (1907), Eifrig (1924), and Allard (1928) have also emphasized the importance of length of day in regulating the migration of birds. Their chief argument is that the regularity of migration from one year to another cannot be explained by normal variations in any other factor except length of day—and so length of day must be the chief factor involved in determining the time at which different species migrate each year.

The length of day varies, of course, inversely with the length of night. A long period of darkness imposes a great tax upon a bird's resistance to low air temperature which may be fatal. Reserve food supplies in the body are utilized and have to be replenished the following day. The number of hours daylight must be sufficiently long to enable the bird to do this. The short days of autumn and winter in the north may not be long enough to allow some species sufficient time for this feeding, and, as a consequence, such species would be unable to survive in the region during that season. Groebels' (1928) emphasis is upon this point.

The effect of different wave-lengths and intensities of solar radiation, particularly of the ultra-violet, on animals has been discussed in a comprehensive manner by Clark (1922) and Laurens (1928) and much of the literature is reviewed in these papers. The field is complicated and difficult, and many of the results obtained are controversial. Only a few of the more significant points in regard to bird activities will be pointed out.

Sheard and Higgins (1930) determined the influence of irradiation by air-cooled quartz-mercury arcs on the incubation of eggs of the domestic fowl. They found that with irradiation the daily loss in the weight of the eggs during incubation was increased, the period of incubation was shortened, and the rate of metabolism of the embryo was increased. In wild species of



birds, the thickness of the shell together with the color of the eggs are factors that must be considered before too much importance can be ascribed to direct solar radiation on eggs in exposed nests.

According to Goodale (1926), the growth of chickens is accelerated by a short exposure of one to three minutes daily to an ultra-violet lamp. Non-irradiated chicks grew more slowly, developed leg-weakness (rickets), and the mortality rate was high. Heuser and Norris (1929) found that an average exposure of 10.9 minutes to direct mid-summer sunshine was sufficient to prevent the development of rickets in chicks and to permit normal growth up to eight weeks of age. It is generally believed in the case of man and certain other animals that the ultra-violet radiation, either by sunlight or by a lamp, activates a chemical compound, ergosterol, in the skin and other tissues of the body, and that this activated compound then influences the calcium and phosphorous metabolism in the body much as does vitamin D. The position of some nests of birds is such that the young may be more or less exposed to direct sunlight for intervals during the day. This may be important for their development. Some species, however, as the house wren, raise their young in semi-darkness entirely protected from solar radiation. In such cases, the necessary vitamins for growth may be obtained from the food consumed.

Ultra-violet radiation, either solar or artificial, also affects adult birds in a marked manner (Hughes and Payne 1924, Hughes, Payne and Latshaw 1925, Hart, Steenbock, Lepkovsky, Kletzien, Halpin, and Johnson 1925, Hendricks, Lee and Godfrey 1931, Maughan and Maughan 1933). Without the proper irradiation and with food low in anti-rachitic vitamin, the calcium and phosphorous content of the blood drops below normal, health is impaired, and hens develop lameness or paralysis of the legs and wings. With two groups of laying hens fed with the same food deficient in vitamin D, it was found repeatedly that the one group which was irradiated a few minutes daily had the advantage over the non-irradiated group in several ways. The egg production was higher, the egg shells were heavier, there was more calcium in the shell and also in the embryo, the yolk contained more vitamin, the fertility of the eggs was not diminished and a larger percentage of the eggs hatched. Sunlight is necessary, therefore, for the proper health of the wild bird, either directly in the proper irradiation of the body, or indirectly in producing the proper vitamin content in the food which they consume.

In man and some mammals, the beneficial effect of solar radiation is only produced when it comes in direct contact with the skin. Some experiments of Goodale (1926) indicate that the feather covering of chickens is not penetrated by the effective wave-lengths of ultra-violet radiation. The usual receptive areas, he believes, must be the exposed parts of the skin, particularly around the head; but in wild birds, there is very little or no skin at all

normally exposed. Maughan (1928) also states that feathers prevent penetration of ultra-violet waves and that the eyes absorb very little or no ultra-violet. One wonders then how this radiation may reach the skin of birds in order to be effective.

Possibly the colors of birds may serve some biological rôle here, allowing beneficial rays to penetrate and reach the skin and to protect the body against other harmful rays. Cartwright and Harrold (1925) and Hadwen (1926) have called attention to the possible biological function of color in animals. Allen (1871) long ago noted that in North America there is a gradual increase in color of birds and mammals to the southward in individuals of the same species. The fact which Allen (1871) and others have noted that birds in humid regions tend to be darker in the color of their plumage than do their relatives in arid localities may possibly be a response to differences in the intensity of the light as well as to differences in the prevailing relative humidity.

Recent studies of Hou (1928, 1929) are of interest in this regard, since he connects the presence and use by birds of the preen gland (*glandula uropygialis*) with the proper effect of irradiation. Birds preen their feathers with droplets from this gland, and much oil is left between the barbs and barbules at the surface of the plumage. Later, after exposure to the sun, these oil droplets are rubbed off by the bill of the bird and swallowed. A chemical analysis showed that this oil from the preen gland contained a large amount of cholesterol, which contains ergosterol, and a large amount of this same substance can be removed from the feathers. If this concept is eventually proved to be true, this will go far towards explaining how birds are successfully irradiated by the sun, and how they may obtain the anti-rachitic vitamin so necessary for health. Hou found that experimental removal of the preen gland from adult birds produced in some (fowl and duck) a marked disturbance of the plumage and an impairment of general health and in others (pigeons) only a slight disturbance of the plumage. Removal of the preen glands from young rachitic or normal fowls produced permanent rickets in spite of subsequent normal feeding, environment, and sunshine. Rowan (1928), in supporting this concept, gives further evidence indicating that in some species of hawks and owls, feathers must be fed to the young during growth in order to prevent rickets.

Certain experiments of our own with nestling house wrens suggest that feathers are useful in the summer in another way, not only for conservation of body heat, but also for protection of the body against the heat energy and possibly harmful rays of the solar radiation. Two naked young birds when exposed to the direct sunlight died within 15 minutes. Another young bird which was feathered was not killed even after a much longer exposure. Different colors in bird plumages may also be important in the heat regulation of the body. The shading of altricial young by their parents during hot after-

noons is necessary for protection against too intense irradiation from the sun. Too intense irradiation by ultra-violet light is also recognized as distinctly harmful by retarding growth or producing other injury, whether it acts directly on the bird or on the food that it consumes (Goodale 1926, Laurens 1928, Price 1926).

Generally, then, an increase in the length of the light period of the day and a moderate, but not excessive, amount of solar irradiation is beneficial and favorable for the best activities of birds.

#### RELATION TO DISTRIBUTION

*Hours of sunshine*—Climographs were prepared for optimum breeding and wintering areas of the eastern house wren including the summer and winter months only (Fig. 24). Total hours of possible sunshine per day are plotted against total hours of actual sunshine per day. The total hours of possible sunshine per day during different months of the year were determined from Table 87, *Smithsonian Meteorological Tables*, 1918, using the figures for the declination of the sun given in Table 88. The percentage of possible sunshine that actually occurs each month is recorded for many stations in *Climatological Data of the United States by Sections*, U. S. Weather Bureau. The actual number of hours of sunshine may then be readily figured when the total number of hours of possible sunshine is known. Data from some stations are available since 1921, but not from others until later. Ottawa, Toronto, New Haven, and Washington, D. C., were omitted, but the other eight regular stations for the breeding area of this bird and all five stations in the wintering area were used. The number of hours of actual sunshine per day is always less, of course, than the number of hours of possible sunshine, because cloudy and foggy weather occur in all regions at all times of the year. The climographs represent then the range in actual and total possible hours of sunshine per day occurring in the two areas while the house wren is present. The summer time is much the more favorable time of the year.

Though the house wren breeds in New England, it is not common there. From Figure 20, one sees that the seasonal march of sunshine for that region falls outside the boundaries of the climograph, as the number of hours of actual sunshine is small. In more northerly regions, the total possible length of daylight greatly increases during the summer, until, within the Arctic circle, the sun never sets. However, cloudy weather may reduce the number of actual hours sunshine. Shorter nights and longer days should be advantageous to the bird, and so the number of possible hours of daylight during the summer should not be a limiting factor in the northward spread of the species in its breeding range, although a reduced number of actual hours of sunshine may exert some influence.

At Louisville, Ky., the house wren is uncommon in the summer and the monthly march (Fig. 20) for that locality goes outside the climograph in July and August. At Nashville, Tenn., and Birmingham, Ala., where the species is entirely absent during the summer, only the month of August falls outside the climograph, although not very far. At Raleigh, N. C. where the bird is also absent, the number of hours sunshine is low throughout the summer. Reference to Figure 24 shows that the daily amount of sunshine in the wintering area of the bird during the summer months is low, although June and July fall inside the limits of the climograph. The fewer number of hours sunshine per day may exert some influence in determining the distribution of the species southward, but other factors probably become limiting for the species before the daily amount of sunshine does.

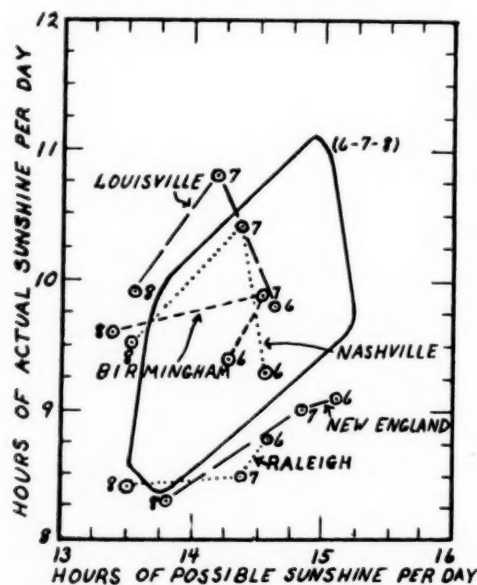


FIG. 20. Climograph of total possible and actual number of hours of sunshine per day for the breeding season (months 6-7-8) of the eastern house wren together with the monthly march in New England and Louisville, Ky., where the species is uncommon; and in Nashville, Tenn., Birmingham, Ala., and Raleigh, N. C., where it is absent at this season.

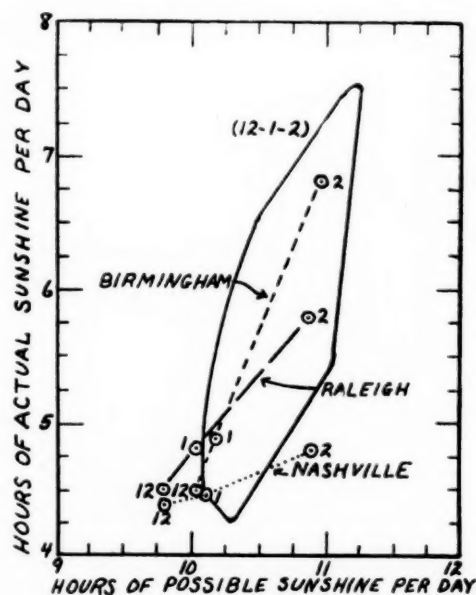


FIG. 21. Climograph of hours of total possible and actual sunshine per day during the wintering season of the eastern house wren together with the monthly march of sunshine at Birmingham, Ala., and Raleigh, N. C., where the species is uncommon; and at Nashville, Tenn., where it is absent.

West of the breeding area, at Lincoln, Neb., Denver, Colo., and Portland, Ore., there is approximately the same amount of light during all months of the summer as there is in the breeding area of the bird itself. At Portland, Ore., there is more than the amount to which the species is normally accustomed. The amount of light daily is not correlated with the subspecies westward.



In winter, the number of hours sunshine per day decreases northward. At Birmingham, Ala., and Raleigh, N. C., where the species winters, although not commonly, one or more months fall outside the limits of the climograph (Fig. 21). At Nashville, Tenn., where the species does not occur at all during the winter, all months are unfavorable. Reference to Figure 24 shows further that the breeding area has very much shorter periods of daylight during the winter than does the wintering area. The number of hours sunshine per day thus appears to be an important factor in limiting this species northward during the winter season.

*Intensity of sunshine*—Figures 22 and 23 show the relative amount of solar energy throughout the year in the breeding and wintering areas. Forty degrees latitude was assumed to represent about average conditions for the breeding area. Likewise, thirty degrees latitude was taken as about average for the wintering area. The data for these figures were obtained by computation, using Tables 88, 91, and 93 from the *Smithsonian Meteorological Tables*, 1918; Publication No. 201 of the Hygrographic Office, 1919, entitled *Simultaneous Altitudes and Azimuths of Celestial Bodies*; and Table XVIII from C. G. Abbott's book, 1929, entitled, *The Sun*. In this computation was involved the use of the *solar constant*, variations in the actual solar radiation received by the earth outside its atmosphere during different months of the year, the air mass through which the solar radiation must penetrate to reach the earth's surface at different times of the year, and the loss in solar energy as it penetrates through this air mass. The energy of the solar radiation was computed in terms of calories per square centimeter per day and calories per square centimeter per minute. Complicating factors of cloudiness, dust in air, indirect radiation, time of day, and other items, enter in, however, that render the figures obtained of relative significance only.

During the winter, the house wren receives more radiation from the sun (calories per day) in the south, than it would if it remained in its breeding range throughout the year (Fig. 22). This is advantageous to the bird. In summer, the breeding area receives more solar radiation during June and July than does the wintering area. The difference is small, however, and during the rest of the summer, conditions are reversed. There is, on the average, 4% more cloudiness in the south during these two months than in the north. This would increase the advantage of the northern region for nesting purposes.

The measurement of ultra-violet radiation from the sun is difficult and little information is available. According to the work of Dorno in Switzerland (quoted by Clark 1922), there is considerable variation in the amount of ultra-violet light reaching the earth's surface not only at different times of the day but also at different times of the year. It is much greater during

the summer than in the winter, and also much greater during the middle of the day than at other hours. These results are confirmed by Clark (1930) and Earp (1929, 1930). According to Clark (1930) the anti-rachitic value of direct sunshine in July is 14.5 times greater than it is in December. In spite of the low ultra-violet content in winter sunshine, there is still sufficient to maintain, in the domestic fowl, the egg production and fertility at a high level (Sheard and Higgins 1930) and to prevent rickets from developing in growing chicks (Goodale 1926, Laurens and Mayerson 1930).

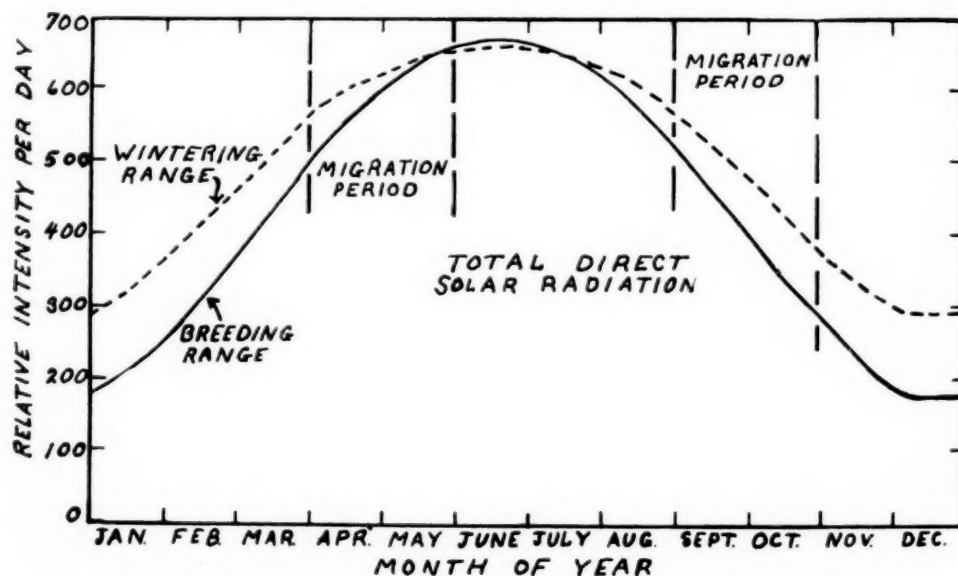


FIG. 22. Relative intensity of the solar radiation per day during different months of the year in both breeding range and wintering range of the eastern house wren.

Although Figure 22 represents the relative amount of solar radiation received in a day at the two different latitudes, it does not give as true an idea of the actual intensity of the sunlight as does Figure 23. This is because all computations are made on the basis of a twenty-four hour day for the sake of comparison, and the difference in the relative length of time that the sun shines each day at different times of the year between the two latitudes is not taken into consideration. Direct solar radiation can only reach the earth's surface when the sun is above the horizon. Therefore, if the values used in Figure 22 are divided by the number of minutes sunlight during the day, the relative intensity of the solar radiation per minute may be obtained.

Figure 23 is of unusual interest since it brings out the fact clearly that the actual intensity of the sunlight is much higher in the wintering range of the house wren at all times of the year than it is in the breeding range. There is more difference in the winter between the two, however, than in the summer, and this is in favor of the wintering area. A certain intensity of sunlight is probably optimum for the house wren. This may be somewhere be-

tween the intensity in the breeding area in June and July, when it is greatest, and the intensity in the wintering area in December when it is lowest, or this whole range may represent an optimum, or at least a range of tolerance. It may be inferred also, although inconclusively, that in the breeding area during the winter, the intensity of the solar radiation drops below this optimum range for the species, while in the summer months in the south it may go above. More research is necessary on this point.

Considering Figures 22 and 23 together, the southward distribution of the house wren in its breeding area may be influenced during the summer by the greater absolute intensity of the sunshine. Likewise, the northward distribution of the species in the south during the winter months may be influenced by the low intensity prevalent in the north.

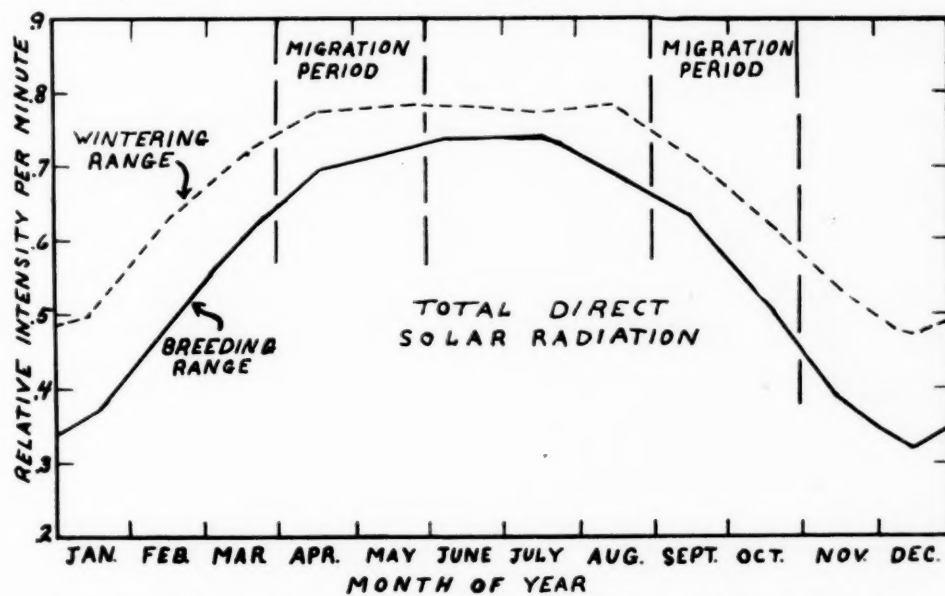


FIG. 23. Relative intensity of the solar radiation per minute during different months of the year in both the breeding range and the wintering range of the eastern house wren.

As for the intensity of the solar radiation in the extreme north during the summer months, there is little direct evidence. Possibly, the total radiation daily received is greater than in the south because of the greater number of hours daylight, and the actual intensity is less because of the lower declination of the sun. Kestner (1927) and Kestner and Borchardt (1928) found that, on clear days and at equal zenith distances, the ultra-violet radiation from the sun is more intense in northern than in middle Europe.

The intensity of the solar radiation may not influence to any great extent the distribution of the eastern house wren westward. Earp (1929) found that direct ultra-violet radiation was about the same during the summer at

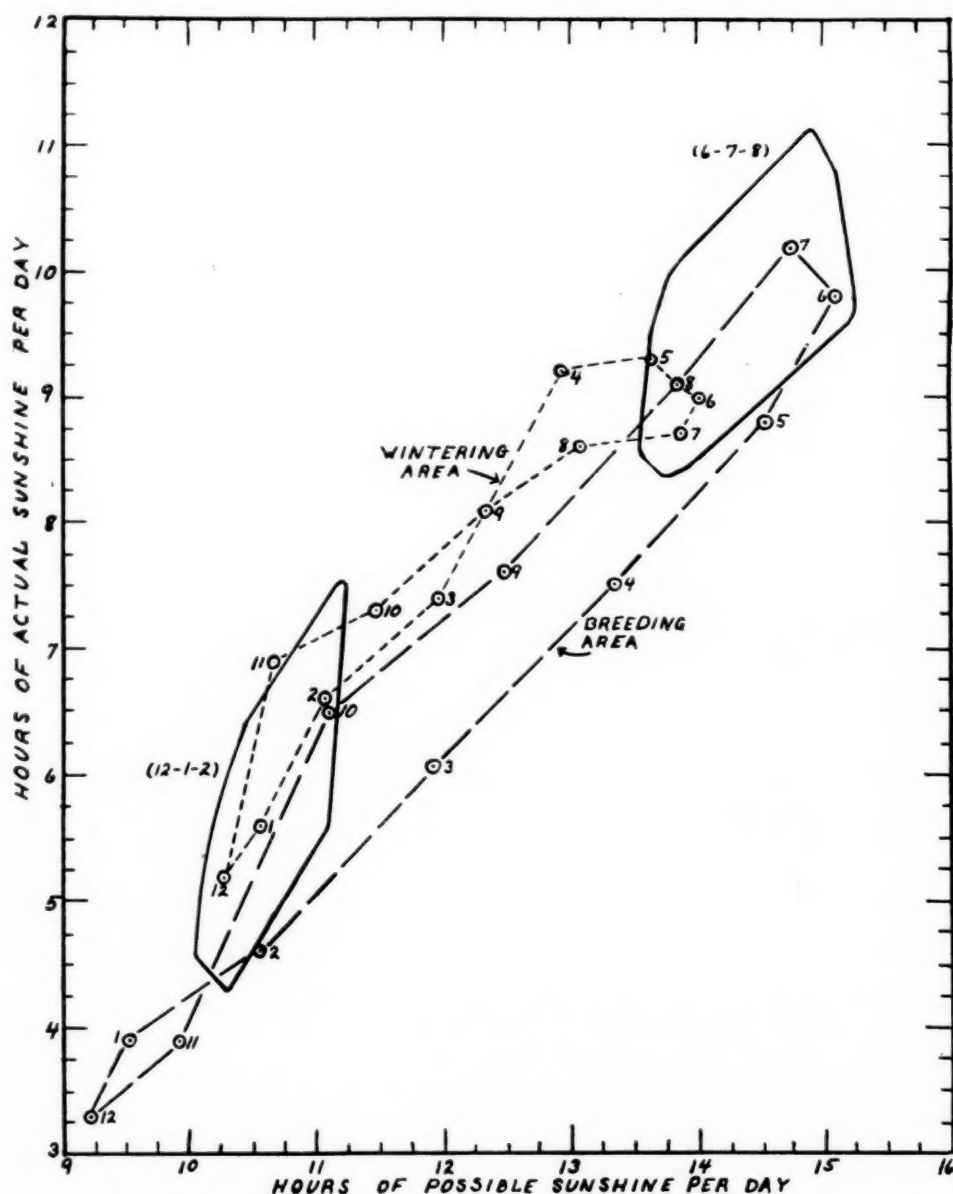


FIG. 24. Climographs of total possible and actual number of hours sunshine per day to which the eastern house wren is subjected during the breeding season (months 6-7-8) and wintering season (months 12-1-2), together with the average monthly march of sunshine throughout the year in both the breeding and wintering areas.

Boulder, Colorado, as at Baltimore, Maryland, but about three times greater in the winter.

#### RELATION TO MIGRATION

The monthly march of sunshine throughout the year for both the breeding and wintering areas is shown in Figure 24. This was obtained for the breeding area by averaging the total hours of possible sunshine in northern



Michigan and Richmond, Virginia, which are near the northern and southern boundaries, to get an average of the total number of hours possible per day. The actual number of hours of sunshine per day is an average for eight stations. For the wintering range, the total number of hours of possible sunshine per day is an average for Montgomery, Ala., and Tampa, Fla., while the number of hours of actual sunshine per day is an average for five localities.

It will be noted that the entire march of sunshine for the wintering area of the house wren never becomes extreme. The months of May, June, and July fall within the climograph for the breeding season (6-7-8), although August is low. From this, one would surmise that, as far as existence alone is concerned, the wintering area might do for all seasons of the year. The added activities of nesting, however, make the northern breeding area more favorable during the summer months because of the greater number of hours of sunshine. The march of sunshine for the breeding area, however, goes below the winter climograph in November, December, and January and this would be unfavorable for the bird during the colder part of the year. By migrating north in the spring and south in the autumn, the house wren takes advantage of the longest daylight periods in each region and avoids the unfavorable shorter periods.

It is in the months of April and May (4, 5, Fig. 24), that the bulk of the house wrens leave the wintering area, migrate north, and enter the breeding area. It is in April that the number of hours of possible sunshine per day first become greater in the breeding area over what it is in the wintering area, although the actual number of hours sunshine is still less. Apparently the bird is affected by the lengthening of the days in spring and migrates at the time that is most advantageous. The same thing is true in the autumn. The house wren leaves the breeding area during September and is within the wintering area by the last of October. A reference to Figure 24, shows that the total number of hours possible sunshine per day is about the same in the two regions during September (9), although the number of hours of actual sunshine is less in the breeding area. In October (10), the wintering area has both the larger possible and larger actual number of hours sunshine per day. It seems, then, that the relative lengths of day and night may have some influence in regulating the time of the bird's north and south migration.

As far as the intensity of the sunshine is concerned, the bird arrives in the breeding area in the spring a little before the time that the total daily radiation becomes practically the same in both regions (Fig. 22). In the autumn, the bird begins to leave the breeding area in September, soon after the total radiation in the north becomes appreciably less than in the south. In Figure 23, showing radiation per minute, the bird leaves the wintering area in the spring at the time when the direct intensity may become unfavorable,

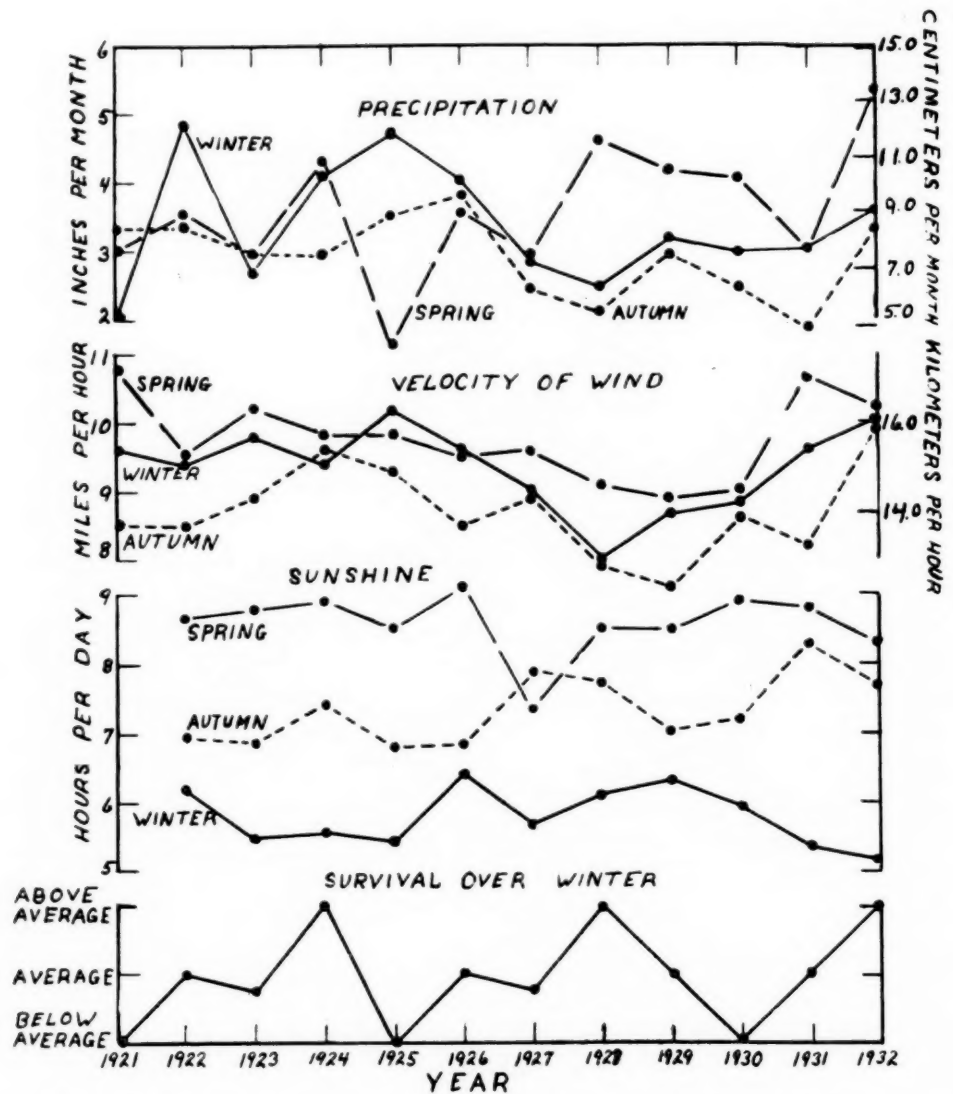


FIG. 25. Correlation between yearly variations in relative amount of survival of the eastern house wren over winter and seasonal averages of various climatic factors to which the species was subjected.

and does not return to the area in the fall until after it drops below this level. The correlation between migration and the intensity of the radiation seems too indefinite and uncertain, as yet, to be considered primarily concerned in regulating the time of these movements.

#### RELATION TO ABUNDANCE

The daily amount of sunshine in the Cleveland region is plotted in Figure 18. No correlation with the amount of reproduction is evident. The amount of sunshine varies inversely with precipitation and relative humidity.

In Figure 25, the daily amount of sunshine during the autumn, winter, and spring is plotted with the relative rate of survival over winter. Data for most localities are lacking for 1921. Taking the sunshine curves for fall and winter together, a loose correlation with the rate of winter survival can be worked out. The curve of sunshine for the spring months appears to be without significance.

## VI. FOOD

Stevenson (1933) made a special study of the food requirements of some passerine birds at the Baldwin Bird Research Laboratory. He found that passerine species of birds during the breeding season usually have some food in their stomach during all the daylight hours, and so digestion goes on continuously. However, during active migration, Groebbels (1930) has found that after a long flight the stomachs of birds are empty. They then rest until they can replenish their resources before renewing their journey.

The rapidity of digestion is indicated by the fact that a morsel of food may pass through the alimentary tract and the undigested portion eliminated in one and a half hours. A full stomach in a song or field sparrow may be entirely digested in two and a half hours. Seed-eating birds eat an amount of air-dried food daily during the summer equal to about 10% of their own body weight. Ninety percent. of the vegetative food eaten by seed-eating species is absorbed, so there is little waste. Insectivorous species may consume an amount daily up to the equivalent of 40% of their body weight, but much of this is water. Rörig (1905) made a special study of several native European species of birds kept in cages during the winter. He allowed these birds all the meal-worms that they could consume and found that they ate an amount daily equivalent in *dry* weight to 8 to 14% of their own body weights. The dry weight of meal-worms he takes to be 40.24% of their fresh weight. Therefore, both insectivorous and herbivorous birds appear to consume in equivalent dry weight the same relative amount of food. According to Groebbels (1931), small birds require proportionally more food than larger ones, due apparently to higher rates of metabolism. In a later work, Groebbels (1932) has exhaustively treated the rôle of nutrition in birds and the bearing that this has upon bird migration and distribution.

The vitamin content of the food which birds eat is important. As much of the research on vitamins has been with the domestic fowl and pigeon, the general findings in this field are applicable to birds. Vitamin D is of special interest since the equivalent effect of this vitamin in food may be produced through ultra-violet radiation upon the animal. This was discussed in the section on Solar Radiation. Rowan (1931) has given consideration to this subject in relation to bird migration. Heape (1931) has recently expounded a theory of bird migration, explaining that birds go north in the spring in order to procure food with the proper vitamins that will stimulate the devel-

opment of the reproductive processes. Bissonnette (1932) has also indicated the importance of food in the spring development of the gonads. Some experiments of Price (1929) seem to indicate that young chicks have a natural ability to choose a diet having a high content of the requisite vitamins. During a period of 57 days, 40 chickens consumed 415 grams of butter high in vitamin A and D, 289 grams high in A and low in D, and 209 grams low in both A and D. If it is true under experimental conditions that the birds select food of proper quality, it may also be true in nature. How much this factor may be involved in controlling distribution and migration is questionable.

The length of time which birds can live without food under different conditions is discussed in the section on Temperature. Stevenson (1933) found that twice as many birds came to the bird-banding traps after food at daily mean temperatures below 75°F. (23.9°C.) as did at temperatures of 81° to 85°F. (27.2°C. to 29.4°C.). This indicates that under natural conditions birds feed more on cold days than on hot days. This is, apparently, in order to compensate for their increased body metabolism and consumption of reserve food supplies in the body.

Some species change from an insectivorous diet in the summer to a herbivorous one during the winter months. Seed-eating species have the advantage over insectivorous ones in the winter because insects are in hibernation and are difficult to find. In Rörig's experiments (1905) with feeding birds in cages, he found that birds consume more food during the summer than during the winter. He explains this on the basis that the days of summer, having more hours of sunlight, permit longer activity by the birds, and as a consequence they consume more food. Groebbels (1931) obtained similar results.

Rensch (1931) has made some interesting comparisons in the anatomical structure of birds in the tropics and in the north temperate zones in relation to their requirements for food. He finds that northern birds possess larger stomachs and longer intestines, which is probably correlated with the necessity for digesting a larger amount of food and at a faster rate.

Snow and ice are frequently disastrous to birds in the winter because food is hidden. Regular winter species in northern regions are ordinarily accustomed to feed on material not easily obscured by snow. In this respect, the tree-trunk climbers have the advantage. When snow is absent, food may be found easily by some species in winter, but during stormy periods they congregate in areas where food is abundant or left exposed (Gillespie 1931, Hicks 1932). If such areas are not available, the mortality rate may become very high (see Behavior Responses under Temperature). Low air temperature may have an indirect effect on birds by making food unavailable, by sending, for example, insects into hibernation.



The consumption and need for food while migrating must be great because of the amount of energy dissipated. Most of the small birds migrate at night so that they may have the daylight hours for feeding. Those species which are able to feed as they fly frequently migrate by day.

Aside from the food requirements of the adults, the amount required for the development of nestlings is tremendous (Groebels 1931). This food is largely insectivorous. A nest full of young passerine birds is frequently fed more than a hundred times a day. In one nest of a house wren containing five young birds, the number of visits with food made by the adult birds per day was 165 the first day, 236 on the second day, while the maximum was reached on the thirteenth day with 349 visits. One of the fundamental reasons for the setting up of "territories" by birds during the nesting season is to assure them of a constant and easily accessible food supply for the young.

House wrens are almost entirely insectivorous in their food habits. Those organisms preyed upon most commonly are species of spiders, caterpillars, grasshoppers, crickets, weevils, leaf beetles, bugs, ants, and other hymenopterans (McAtee 1926). The house wren is, without doubt, influential in controlling the abundance and to some extent the composition of the insect forms of the biotic community in which it lives.

According to unpublished data of Rutherford and of Stewart, formerly of the University of Illinois, the bulk of the insect life in deciduous forest communities comes out of hibernation in the latter part of April and returns in the first part of October. While hibernated, they are not so easily found, but during the summer months they are active and reproduce rapidly so that they become abundant. The time of emergence corresponds to the time that the house wren returns to the region, and likewise, the time that the insects go back into hibernation in the fall is not long after the house wren leaves. This indicates that the migration of the house wren is still further adjusted to the advantage of the species in that it is present in the breeding area only during the maximum abundance of its insect food. Southward, in its wintering area, the weather does not necessitate as much insect hibernation, and thus existence there during the winter is less hazardous than in the north. Likewise, there is no snow to cover up what food may be present. Davis (1933) and Linsdale (1933) have made detailed studies of nesting dates of various species of birds and find this closely correlated with the time food becomes available, which in turn is dependent upon the climatic conditions of the region.

Some investigators have considered the availability of food as the essential factor involved in driving the birds south in the fall and bringing them north again in the spring. They claim that there would not be enough food in the tropics to supply all the individuals that winter there throughout the nesting season if all of them nested, and that some of the birds are forced to migrate

north in order to obtain a sufficient supply. One cannot see how the availability of food in the north could alone determine the constant regularity of migration from the south year after year and both the time and extent to which birds migrate. On the other hand pine grosbeaks, *Pinicola enucleator leucura* (Müller); crossbills, *Loxia* spp.; red-breasted nuthatches, *Sitta canadensis* Linnaeus; snowy owls, *Nyctea nyctea* (Linnaeus) and other species of northern birds migrate south only during those winters when the food supply in the far north fails. Undoubtedly this food factor is an important one also with other species in the autumn that migrate regularly, and may in some cases, be the chief factor involved. Most of the house wrens leave before the insect population is entirely reduced in October, and so are not actually forced out, but the decreasing abundance of insects may be partly regulatory of the time that the birds leave. Seed-eating species would not be thus affected.

There is a fluctuation in numbers of insects from year to year. This may have some effect upon the abundance of birds. Generally, however, birds "select from that which is available," and so unless there were decided fluctuations in the total insect population, the abundance of the birds would not necessarily correspond with fluctuations in numbers of any particular species of insect. Little information is available on this point for correlation with fluctuations in the number of house wrens. There is probably also a difference in total insect population between different communities and different parts of the country, but until definite comparable data become available, little can be stated as to the effect that this may have upon bird distribution.

## VII. PRECIPITATION AND WIND

For convenience of discussion and because there is some natural relation between precipitation and wind in their effect upon bird life, these two factors will be considered together.

### PHYSIOLOGY AND BEHAVIOR RESPONSES

*Precipitation*—Precipitation, either in the form of rain or snow, frequently has a great effect upon birds. The feathers of water birds are usually oiled sufficient that they can swim and dive without becoming watersoaked. The feathers of land birds overlap sufficiently and are also oiled so that they shed water. Ordinary rains, therefore, do not wet adult birds to any harmful degree, although severe storms may kill some birds by soaking the plumage and forcing them down sometimes to be drowned (Childs 1913, Morton 1902, Bennett 1909, Saunders 1907, Reagan 1910). Hail storms occasionally do heavy damage (Gates 1933). Barrows (1889) recites accounts where the English sparrow was killed by hundreds during severe storms accompanied by heavy winds. If the plumage once becomes soaked, loss of body heat is

accelerated, and death may occur rapidly. This has occurred accidentally on a few occasions in our experimental work.

Juvenile birds, even several days out of the nest, are less able to avoid becoming soaked by rains than are the adults. Heavy rainfall during the summer months may destroy many individuals. Nestling birds and eggs are usually protected during rain storms by the brooding of the adults, but if they become wet, death usually occurs in a short time. Even in the case of eastern house wrens, which nest in boxes, water sometimes runs in during heavy rains and soaks the young and nest. In one instance, a nest and set of eggs became thoroughly wet in a storm and the adult birds deserted at once. In another instance, however, the adults returned and later hatched the eggs. Poultry raisers no longer advise washing eggs before placing them in artificial incubators. Nests are frequently washed down and destroyed by heavy down-pours. Floods are, of course, disastrous. Heavy rains during a nesting season may be so serious for the bird population that recovery may not take place for several years (Cooke 1923, Saunders 1919).

Rainfall, particularly when combined with low temperature, may affect the food supply. Frequent rain storms may clear the air of insects so that chimney swifts, *Chactura pelagica* (Linnaeus), and swallows suffer (Forbush 1927). When the precipitation falls as snow much of the same effect occurs. In addition, the ground becomes covered with a blanket that hides the food supply. Heavy snowfalls occurring late in the spring and early autumn are especially destructive because they affect species not ordinarily subjected to them.

In the arid southwestern part of the United States, rainfall is of considerable importance in affecting the reproduction of quail and other game birds. According to Grinnell (1927), broods of young California quail, *Lophortyx c. californica* (Shaw), must be within walking distance of drinking water within a few hours after hatching, if they are to survive. During years of drought, few young are raised, adult birds tend to remain in flocks, and there is little development of the gonads. On the other hand, years with high rainfall show exceptionally high reproduction of birds (Grinnell, Bryant, and Storer 1918). A similar relation between amount of precipitation and reproduction apparently holds true also in Tunis, where Lavanden (1927) found that in years of extreme drought partridges do not nest and their gonads remain undeveloped. Likewise in Queensland, similar reports occur (Berney 1928). Drought is, therefore, especially serious with birds in desert and semi-desert regions. Nice (1933) suggests the possibility that even with a passerine bird in a humid region an unusually dry summer may curtail nesting and hasten molting. Schneider and Schneider (1928) found in other regions that the barn owl, *Tyto alba* (Bonaparte), raises more broods during dry seasons, that favor the breeding of mice, than during normal years. Ap-

parently the effect of precipitation upon the amount of reproduction is indirect through regulating the amount of available food.

*Wind*—Wind has various effects in relation to bird life. Frequently, rain and snow storms are accompanied by severe winds and then the destruction is worse than if either occurred alone (Barrows 1899, Forbush 1921). Trees may be blown down, limbs broken off, and nests torn loose. During heavy winds birds are usually inactive and seek shelter. Even the heaviest and most expert flying birds then have difficulty making way against strong winds. During migration, birds may be blown several miles off their regular course. This is more perceptible in coastwise migration, because birds, which usually migrate several miles offshore and are seldom seen near land, may appear in numbers during an onshore wind. Small land birds of weak flight do not often get far above the ground. Some birds, as vultures and hawks, are expert fliers and take advantage of air currents and weak winds.

Winds are usually cooling. They may ruffle the bird's feathers and increase the circulation of air around the body. This is of advantage at high air temperatures because it increases the conduction of heat away from the body and also increases the possibilities for evaporation of water with the consequent loss of heat. Evidence was furnished in experimental work (Table 11) that subjection to wind decreases the survival time of birds at medium or low air temperatures, and this is due to the excessive cooling produced, as well as to the probably greater exertion of the birds during a wind.

Various degrees of importance has been attached to the direction of winds in bird migration. Eagle Clarke (1912, p. 178) emphatically insisted that their direction, apart from the weather conditions to which they are due, has no influence whatever upon movements of birds, although high winds from any quarter are unfavorable. A. H. Clarke (1905), however, proposes a rather ingenious theory, based entirely upon the prevailing direction of the wind, to explain the remarkable migration of the golden plover, *Pluvialis d. dominica* (Müller), over the pathless sea.

#### RELATION TO DISTRIBUTION

A climograph, shown in Figure 26, was prepared using velocity of wind and amount of precipitation for the various stations in the optimum breeding and wintering areas of the eastern house wren during the periods that the species occurs in each. This climograph shows that the species tolerates very wide limits both in monthly rainfall and mean monthly velocity of wind. There was no evidence that either factor, alone or in combination, has any influence in limiting the breeding and wintering areas of this species in either the northward or southward direction.

At Lincoln, Nebraska, conditions are optimum during the summer as far as these two factors are concerned (Fig. 26.). At Denver, Colo., the rainfall is low and becomes very scanty in September. At Portland, Ore., it is



outside the limits throughout the summer. The wind velocity is low in both of these latter localities. As far as the direct effect of rainfall is concerned, both of these latter places would seem favorable. However, the effect on the bird of a lack of rainfall may be indirect by influencing the food supply or by controlling the relative humidity. The eastern house wren does not occur at either of these two places nor at Lincoln, but the western house wren does. Although the western subspecies is subjected to drier conditions than the eastern form, a decrease in rainfall does not appear to be a sharply delimiting factor separating the two subspecies, as it is still moderate as far west as Lincoln.

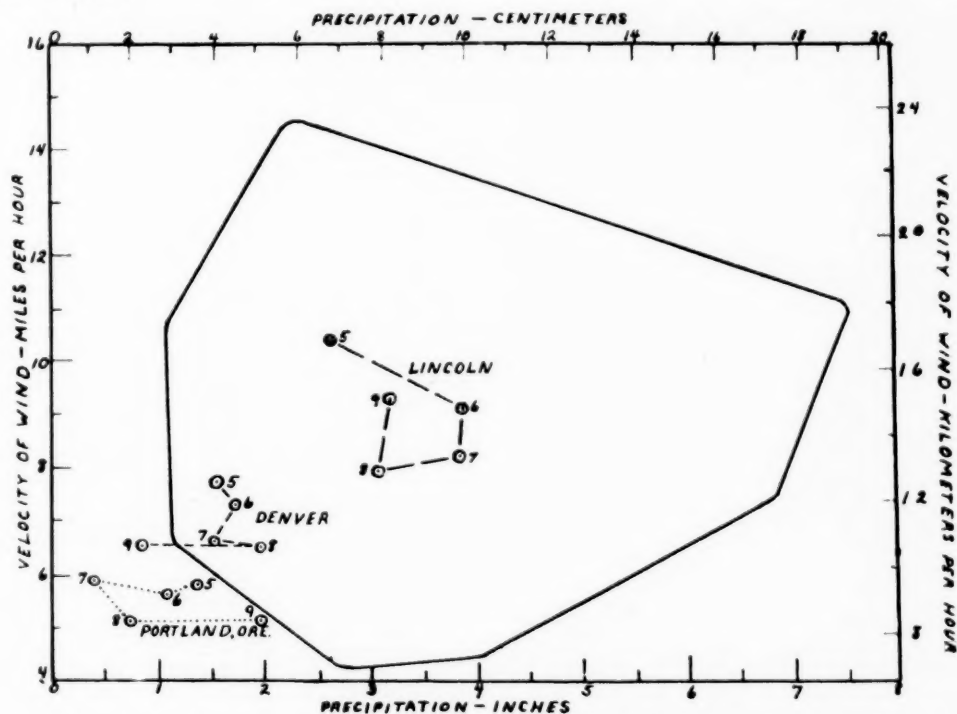


FIG. 26. Climograph of average monthly precipitation and average monthly velocity of wind to which the eastern house wren is subjected throughout the year, together with the average monthly march of these factors during the breeding season at Lincoln, Nebr., Denver, Colo., and Portland, Ore., where the eastern subspecies of the house wren is replaced by the western subspecies.

#### RELATION TO MIGRATION

In Figure 27, the monthly march throughout the year for both the breeding and wintering areas are shown. It will be seen that precipitation is higher in the wintering area than in the breeding area at all months of the year except April and November. During the summer the difference is pronounced. The house wren avoids this by migrating north to spend the summer. The precipitation in the north in the winter is mostly in the form of snow, so by migrating south in the autumn this is also avoided, and the bird

has the advantage of being in either region during the most favorable season of each.

The velocity of the wind is, in general, some little higher in the north than in the south during the winter. This a further advantage to the bird, therefore, in migrating south in the fall. During the summer, however, the wind velocity is about the same in both the wintering and breeding areas.

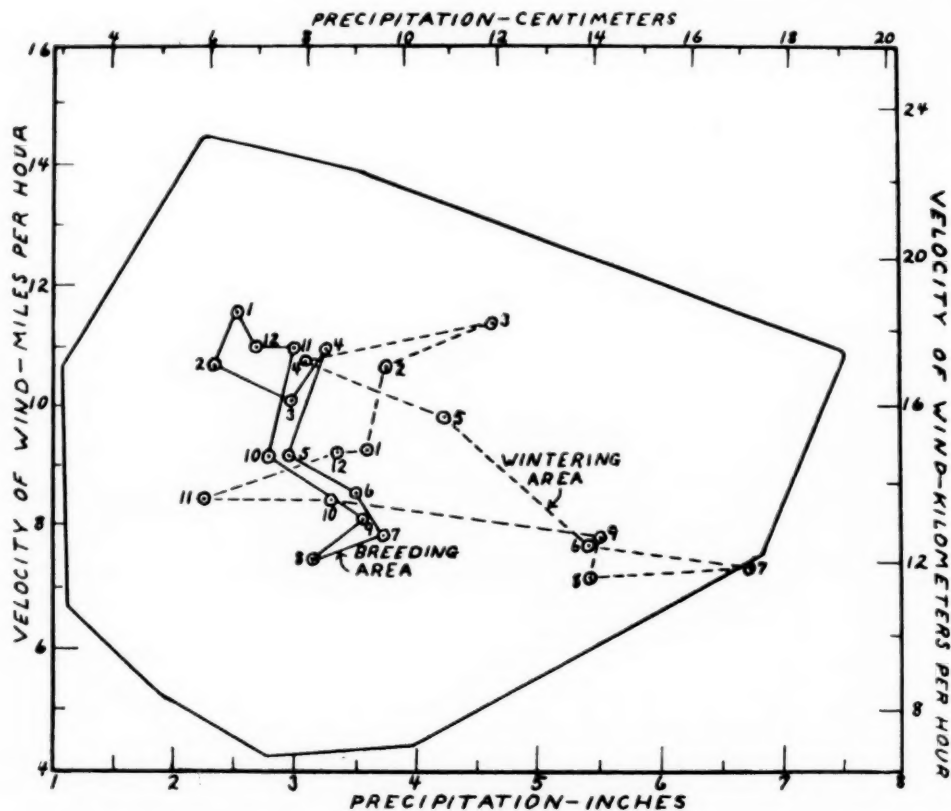


FIG. 27. Climograph of average monthly precipitation and average monthly velocity of wind to which the eastern house wren is subjected throughout the year, together with the average monthly march of these factors in both the wintering and breeding areas.

#### RELATION TO ABUNDANCE

No correlation at all could be found between precipitation and amount of reproduction from year to year (Fig. 18). A slight inverse correlation exists, however, with velocity of wind. During the five years in which the amount of reproduction was above average, the velocity of the wind averaged 10.3 miles (16.6 kilometers) per hour. During the five years when the amount of reproduction was approximately average, the velocity of the wind was 11.0 miles (17.7 kilometers) per hour, while during the three years with reproduction below average the wind velocity was 11.1 miles (17.9 kilo-

meters) per hour. A high wind may be important in aggravating the effect of low air temperature upon the metabolism of the bird.

In Figure 25, the average monthly precipitation and velocity of wind during the fall, winter, and spring are plotted. The curves for precipitation in fall and winter permit no consistent correlation with the rate of winter survival. The precipitation curve for the spring shows, however, a distinct positive correlation, except in 1931 and possibly 1930. This correlation is contrary to what one might have expected, but may indicate that a higher precipitation in the spring may induce an earlier and more rapid development of food and thereby have a favorable indirect effect upon the number of birds that survive. The velocity of wind during the winter and spring shows some tendency to fluctuate inversely with rate of winter survival. This correlation is not consistently close during every year but is sufficient to indicate a possible secondary influence through aggravating the effect of low air temperature.

#### VIII. BIOTIC INTERACTION AND COMPETITION

The competition between the eastern house wren and other birds for territory and nesting sites is often severe. The house wren is an audacious bird and is usually successful in these struggles, but not always. The competition takes the form of actual body combat, destruction of nests, puncturing of eggs, and throwing out of eggs and young from nests to the ground below. Some individual house wrens are more pugnacious than others, while some are so docile as to allow other species, notably eastern robins, to build in very close proximity. The list of species with which the house wren comes into competition is long, but the evidence is convincing, as in many cases there has been actual observations of the destruction of other birds' nests. The following species are known to be involved (*Bird-Lore*, *The Wilson Bulletin*, 1924-1927): mourning dove; eastern phoebe, *Sayornis phoebe* (Latham); crested flycatcher, *Myiarchus crinitus* Bangs; eastern cardinal; scarlet tanager, *Piranga erythromelas* Vieillot; English sparrow; chipping sparrow; tree swallow, *Iridoprocne bicolor* (Vieillot); purple martin; Carolina chickadee, *Parus c. carolinensis* (Audubon); black-capped chickadee; tufted titmouse; Bewick wren, *Thryomanes b. bewicki* (Audubon); bluebird; and robin. Nine of these species nest in similar cavities as does the house wren, and much of the competition may be directly for nesting sites. With the other six species, the competition is partly for territory and may be partly without particular purpose. Competition between the house wren and the Bewick wren may be very severe in certain localities with the result that one or the other species is driven out.

Competition with the Bewick wren may explain the rarity of the house wren in parts of Kentucky, southern Indiana (Butler 1891), southern Ohio (Jones 1903), and West Virginia (Sutton 1930). Apparently in Virginia,

the Bewick wren is less common and does not seriously compete with the house wren. Around the southern periphery of the bird's range, where climatic conditions are becoming unfavorable, the house wren appears less able to combat the Bewick wren. The Bewick wren, on the other hand, regularly breeds further south, is apparently better adjusted to the warmer climate, and this gives it an advantage in competing with the northern form. In certain more northerly localities in Pennsylvania, however, the house wren has apparently replaced the Bewick wren (Christy 1924).

Variations in local abundance throughout the breeding territory may be due to unsuccessful competition with one or another of the various species listed above. Likewise, variations in abundance in the same locality during consecutive years may conceivably be due in part to varying amounts of competition with other species which are also fluctuating in abundance. There is no evidence, however, that this was of importance during the years 1921-33.

The common white-footed mouse, *Peromyscus leucopus noveboracensis* Fischer, frequently nests in cavities, holes, and boxes similar to those used by the house wren. When a house wren is active in the possession of a nesting-site, it ordinarily keeps the mouse away, but if the mouse has already established its nest in a hole, it is seldom driven out. Thus, some suitable nesting sites are rendered unavailable to the house wren. Hancock (1911) describes one instance when he found a dead house wren made into part of the nest of a white-footed mouse that was placed in a hole in a dead tree.

Red squirrels, *Sciurus hudsonicus loquax* Bangs, and pilot black snakes, *Coluber obsoleta* (Say), are common enemies of wild birds, particularly of young birds just out of the nest. When house wrens are nesting in natural localities away from human habitation, these two species probably destroy many nests and suck the eggs or kill the young. In the case of those house wrens nesting in man-made boxes, they are protected from the red squirrel by the small size of the entrance hole. Occasionally, however, a pilot black snake will destroy a nest. In the study area of the Baldwin Bird Research Laboratory, both pilot black snakes and red squirrels were abundant in the summers of 1925 and 1926. Many nests of several species were destroyed, although only one nest of the house wren was touched. In 1927, there were fewer snakes, but the squirrels were still abundant. In 1928 and 1929, there were few of either and in 1930 almost none. In 1931 there were more red squirrels, in 1932 they became very abundant along with other rodents, and in 1933 were again reduced in number. A comparison of these variations in number of bird enemies with the relative amount of reproduction (Table I) of the house wren from year to year suggests a possible inverse correlation between the two. While the number of enemies is probably not the most important factor involved, it may conceivably exert some influence upon the



amount of nesting undertaken, through occupation of suitable nesting sites of the birds and harassment in other ways. No correlation between number of enemies and survival over winter can be noted.

The common house cat is another dreaded enemy of birds, but they could not well get at house wren nests in boxes and cavities nor would they be likely to get many young house wrens after they acquired the power of flight. Young birds would be subjected to danger from this source primarily for only a few days immediately after leaving the nest. There are no data available on the fluctuations in numbers of roaming cats from year to year.

Owls and hawks probably do not constitute important enemies of house wrens, since they could not ordinarily reach their nests nor attack them while roosting in dense thickets and vines. When nesting under natural conditions, however, house wrens are probably more subject to their attacks.

Aside from the interspecific competition, there is also a continuous strife between individuals of the same species for nesting sites and territories. This is engaged in principally by males and may become particularly severe when the birds are abundant or nest sites few. Howard (1920) has discussed the territorial relations of birds in a comprehensive manner. The house wren has a territory around its nest which averages about a half-acre in extent. Variation in the size of this territory is dependent on the amount of shrubbery, nesting sites, and food that it contains, and on competition with other individual birds. The house wren carries on nearly all its activities within the boundaries of these territories and seldom goes outside. There is competition between different individual house wrens and with other species for establishing and maintaining these territories. The size of the territory required is one factor involved in determining the abundance of many species of birds in a community. Some investigators believe that this is also a factor in causing bird migration, in that the tropics become too crowded for all individuals to establish nesting territories, and some must move out when the coming of spring makes northerly regions favorable climatically. It is, of course, advantageous for birds to go north in the summer because there is more room there for setting up territories. Southward migration in the fall would not, however, be stimulated by any territorial relationships.

Vegetation is of direct importance to house wrens in three ways, in furnishing shelter, nesting sites, and nesting materials. Thick shrubbery shelters the bird from the hot sun, adverse climatic conditions, the attack of enemies, and serves for roosting places at night. The house wren ordinarily selects hollows, cracks, or cavities in trees for nesting sites, or they may use brush-piles. Man has erected numerous boxes which imitate natural cavities, and these are much used. Other factors being favorable, the abundance of the species is dependent upon the number of nesting sites available. It is common experience of many people to get several pairs of house wrens nesting

about their homes by simply putting up a number of nesting boxes (Grosvenor 1916). The bird is very adaptable, however, and all sorts of unusual locations are selected for building a nest. For nesting material the bird uses that which is available near the site chosen and within the territory. Dead twigs of either deciduous trees or evergreen trees without the leaves are gathered indiscriminately. Frequently nails, hairpins, wire, and other unusual things are used. The nest cavity is then lined with dried grass and feathers. Frequently a piece of cast snake skin is introduced. As far as distribution and migration is concerned, the requirement of particular nesting sites and nesting material is not regulatory.

The close similarity in the distribution of the eastern house wren during the breeding season and the *Acer-Fagus* Association (Figs. 1 and 2) is of considerable interest and might presuppose some intimate interrelation between bird and vegetation that controls the distribution of the bird. The correlation in the northern distributional limits of the two seems to be of special significance since it marks the transition from a deciduous to an evergreen type of vegetation. Just what the factors involved in such a correlation may be, cannot now be stated. The evidence available indicates that any influence exerted by the vegetation must be an indirect one, possibly through some change in the quantity or quality of the food supply.

#### IX. PHYSIOGRAPHIC FEATURES

Physiographic features often constitute barriers for the distribution of birds. Usually, however, the physiographic feature itself acts only indirectly, as by producing an area where suitable nesting places, shelter, and food are unavailable. This is true with large water bodies. In the case of the eastern house wren, the eastern limits of its breeding range are not determined by climatic conditions but by the Atlantic Ocean. Likewise, the wintering range is limited on the east by the Atlantic Ocean and on the south by the Gulf of Mexico. Were the gulf not there, the wintering area of the house wren would extend farther south than it does, as the bird seems to be more common farther south in Florida. Even the narrow straits between Florida and the West Indies are effective, as the species does not cross over. Apparently the house wren does not have a great capacity for long continuous flying.

During migration, physiographic features are undoubtedly of considerable importance in aiding the bird to find its way. Rivers, valleys, lakes, coast lines, mountains, and differences in types of vegetation are probably all important in establishing definite routes of migration. Some of these routes have been mapped. One such representation for Europe given by Clarke (1912) is very impressive in this regard. In North America, the Mississippi valley is the main inland thoroughfare, while the Atlantic and Pacific coast lines are followed by many species.

## X. DISCUSSION AND SUMMARY

The different environmental factors have been discussed singly and in relation to one or two of the others. There remains the necessity for correlating all the factors and giving some evaluation of their relative influence in the bird's life. It will be understood that the discussion applies primarily to the smaller passerine species.

## PHYSIOLOGICAL PROCESSES

The physiological processes continually taking place in a bird are dynamic in nature, not static. The rate and nature of the functioning of the different organs and of the entire metabolism is never quite the same at any two moments. There are two main cycles in these dynamic internal processes—diurnal and annual.

The diurnal cycle of body temperature, metabolism, activity, and the procuring and digestion of food have been discussed. The importance of these cycles that have been mentioned is apparent because they are relatively easy to determine. Other cycles may be fully or even more important, but they are more difficult to estimate. The diurnal rhythm of these processes is probably essential to the well-being of the bird and is of great importance in the bird's adjustment to environmental factors, many of which also possess a diurnal cycle of variation.

The annual cycle extends over a much longer period. It manifests itself in various but particular ways in different seasons of the year. In activities the cycle involves reproduction, migrating, and wintering. Although the manifestations of innate physiological cycles are readily studied, the actual processes forming the basis for them are little known. The gonads vary in size and function in different seasons. The thyroid also varies but in a different way and other endocrine organs may behave similarly. Resistance to low external temperature is greater in the winter than in the summer. Changes in body weight and storage of fat occur with the seasons. Such changes cannot occur without involving the entire metabolism and vigor of the bird. It is desirable, then, to think of the bird as a rhythmically dynamic organism.

Limits of tolerance are manifested in the relation of birds to various environmental factors. Beyond these limits of tolerance, existence is hazardous or impossible. Limits of tolerance have been discovered for low temperature that involves average night temperature and number of hours of darkness, for maximum temperature, for short days, lack of food, too intense biotic competition, lack of nesting territory and nesting-sites, and unfavorable physiographic features. Other factors as solar radiation, relative humidity, precipitation, wind, and type of vegetation are also frequently of importance. Some

of these various factors may likewise exert a significant rôle with the bird indirectly, through modifying the effect of some other factor.

#### BEHAVIOR RESPONSES

The behavior responses of a bird in their underlying tendencies are attempts to adjust between structural and physiological potentialities and external conditions. Habit and other nerve patterns, as well as endocrines, play a directive or modifying rôle in this adjustment. When environmental conditions remain constant, the bird will not behave the same if its physiological state varies. Nor will it behave the same while in the same physiological state if there are changes in environmental conditions. Behavior aims to adjust the bird to surrounding conditions without over-taxing of physiological processes. In order to adequately interpret bird behavior, therefore, it is necessary to understand this interplay between the physiological potentialities and the environment. Similarly, to understand the rôle of environmental factors in the life of birds, one must take into account not only physiological potentialities but also possibilities in the way of compensating responses in behavior.

It is probable that limits of physiological tolerance to environmental factors are seldom experienced by the general population of any species of bird, although portions of the population not infrequently do so. If this were not so, greater mortality would regularly occur and the species might soon become extinct. There is very probably a *zone of physiological discomfort* before the actual limits of tolerance are reached. Birds respond more to these zones of discomfort than to the actual limits of tolerance, and adjust their behavior accordingly. The zone of discomfort would serve as a warning of the approach of dangerous conditions.

#### FACTORS CONTROLLING DISTRIBUTION

When environmental factors approach or go beyond that to which the physiology and behavior of the bird can adjust, they become limiting for the distribution of the species. All environmental factors vary to some extent. Those which vary the greatest and the quickest, in respect to the resistance of the bird, are the most important. No one factor may be most important everywhere for all species. Merriam's attempt (1894) to explain the northward and southward distribution of animals and plants on the basis of certain particular phases of temperature is not now generally accepted (Kendeigh 1932, Shelford 1932). Attempts of Grinnell (1914, 1917, 1928) and Howell (1922, 1924) to explain the limiting effect of the environment on the distribution of birds and mammals have been more comprehensive and have rightfully considered the possibilities of several factors.

*Northward distribution*—In reviewing the rôle of the various environmental factors as they affect the northward distribution of the eastern house



wren during the breeding season, low night temperature and hours of darkness appear to be most important. The decrease northward in number of hours of darkness compensates only in part for the drop in temperature. A correlation is also possible between the northern limits in the distribution of the house wren and the *Acer-Fagus* Association (maple-beech forest), but this is of indirect and of uncertain importance. The northward distribution of the house wren in the winter is controlled by several important factors: low air temperature at night combined with many hours of darkness, shorter daylight periods, lower intensity of solar radiation, snow, and lack of available food. These factors are all more or less interacting, and all are important.

*Southward distribution*—The chief factors which appear of importance in controlling the southward distribution of the eastern house wren during the breeding season are daily maximum temperature and competition with the Bewick wren. Shorter days, greater intensity of solar radiation, and higher relative humidity may also exert some influence, although less is known concerning the latter factors. During the winter, the distribution of the bird on the south is very clearly limited by the Gulf of Mexico.

*Eastward and westward distribution*—The eastward distribution of the eastern house wren both during the summer and winter months is limited by the Atlantic Ocean. The westward limits of the eastern house wren appear to be correlated in some way with the decrease in precipitation and relative humidity. A closely related form, the western house wren, differing from the eastern subspecies only slightly in color, extends to the Pacific Ocean. The boundary between the eastern and western subspecies of the house wren is probably a broad one with intergradation occurring. It is doubtful if the difference in precipitation and relative humidity that has been noted is correlated with any more fundamental difference in physiological responses of the two subspecies than degree of feather pigmentation.

The above summary of data takes in only the factors considered in this report. Other factors may be of importance, but they have been little studied. Until these other factors have been studied in some detail, judgment as to which are the most important can be based only on that information which is available.

#### FACTORS CONTROLLING MIGRATION

The rôle that environmental factors play in controlling the migration of birds needs to be considered from various aspects. Most of the discussion that follows applies directly to the case of the eastern house wren. While it is very desirable that many species be studied separately before generalizations are made, it is probable that many other passerine species are controlled in their migration in much the same way as the eastern house wren.

*Advantages of migration*—If species of birds are to maintain their existence, they must move out of areas during periods when one or more environmental factors get beyond their limits of tolerance. Such is the case with the house wren. The advantages coming to this and other species in migrating south in the autumn and north in the spring may then be listed.

The advantages obtained by moving south out of the breeding area in the autumn are avoidance of low air temperature at night combined with many hours of darkness, avoidance of snow, avoidance of an inadequate food supply, and the obtaining of longer days for activity, a greater amount and intensity of solar radiation, and a lower wind velocity.

The advantages coming to the bird in leaving the wintering area in the spring and returning north are avoidance of a high daily maximum temperature, a high relative humidity, and a possibly too high intensity of solar radiation, and the obtaining of longer days and shorter nights, less precipitation, and less competition for food, territory, and nesting-sites. There are no data available indicating any greater abundance of food available in the north during the summer than in the south.

By migrating, the bird maintains itself under a more nearly constant set of favorable environmental conditions the whole year round. Allen (1871, p. 422) postulated this fact for other species many years ago when he said: "Most of even the insectivorous species visit regions in winter whose average winter temperature differs but little from that of their breeding stations, and when excessive heats of summer and spring arrive in the southern latitudes, they gradually retire again to their northern breeding stations, keeping pace in their migration with the northward advance of the summer warmth."

The main disadvantages which the bird experiences in migrating are the expenditure of energy in traveling so great a distance and the chance that it may wander too far from its migration route and get into unfamiliar territory. However, the many advantages greatly outweigh the unfavorable features, while the evidence is convincing that certain species, as the house wren, would cease to exist, if, for some reason, it attempted to remain on its natural breeding area throughout the year. The ultimate cause for migration is therefore clear.

*Annual regulation of migration*—The factor or factors that actually stimulate birds to migrate and that are responsible for the regularity of the movement year after year, is a different problem from the advantages to the species of doing so. There can be no question concerning the latter. Volumes have been written, however, on the former question and many theories advanced. The more important of these earlier theories have been briefly reviewed by Walter (1908). Since 1908, the most important contributions to the subject have been made by Clarke (1912), Nichols (1918), Howard (1920), Eifrig (1924), Cahn (1925), Thomson (1926), Stanchinskii (1926),

Wachs (1926), Wetmore (1926), Rowan (1929, 1931), Mayr and Meise (1930), Heape (1931), Grinnell (1931), Groebbels (1932), and Stresemann (1933). Many investigators attempt to explain the migratory impulse entirely on the basis of one factor, whether the factor be of physiological, environmental, or psychological nature. Some dismiss it as an "instinct" without further ado. Certain facts and ideas have come to light in this investigation which give a new interpretation to some of the older theories, and which result in an attempt to correlate and harmonize some of the different points of view.

There is no reason to believe that the stimulus for the migration of passerine birds is due to the effect exerted by any one external or internal factor. This is the first point that needs emphasis. Formerly, migration was commonly explained on the basis of temperature alone, as this was the most obvious correlation that could be made with external conditions. During recent years this viewpoint has been much criticized, but usually on casual observational grounds, without detailed analysis of climatic conditions in connection with experiments upon the physiological responses of birds. It is desirable that such analyses and experiments be made for several species of birds representing as many different types as possible. Undoubtedly, the factors involved in inducing migration are not similar for all kinds of birds.

The number of hours of darkness per day is important in any consideration of the temperature factor. This is fully discussed in the preceding pages. Long nights and low temperatures are distinctly unfavorable. Short nights are favorable, and are, of course, inversely correlated with long daylight periods. Long daylight periods are also favorable because they give more time for the necessary reproductive activities, for obtaining food, and for permitting greater accumulation of solar radiation. An analysis of a large number of environmental factors indicates that the relative lengths of day and night and average night temperature are among the most important factors that must be concerned in regulating the time of migration. In the spring, an additional factor, the rising daily maximum temperature occurring in the afternoons, also constitutes an important regulatory factor concerned in northward migration, for, as was shown previously, the high maximum temperatures in the south during late spring and summer are not readily tolerated.

Food must be readily available at all times. This is required for maintaining the temperature resistance in addition to the necessity for supplying body energy. Insects and other food become plentiful in the north by the time the birds arrive in the spring and decrease rapidly in the autumn when the birds leave. The decreasing food supply in the autumn may conceivably afford some regulation of migration of insectivorous species then, although it, in turn, is controlled in amount and time by changes in temperature and length of day. An increasing food supply in the spring in the northern breeding

areas cannot, however, be regulatory for birds to start migrating hundreds of miles southward. Some more immediate and definite stimulus is required. The same argument holds against any effect being exerted by the increased availability, with the coming of spring, of nesting territories and nesting-sites in the north. Other factors such as intensity of solar radiation, velocity of wind, precipitation, relative humidity, and biotic competition and interaction, appear to have minor or no significance in connection with the stimulus for migration, although the full effect of some factors, as the intensity of solar radiation, is not certainly known.

A summary of the available evidence indicates, therefore, that the northward spring migration is regulated and timed in an important manner by increasing night temperatures, decreasing daily periods of darkness, increasing daily periods of light, and increasing daily maximum temperatures. In the autumn, southward migration is regulated by decreasing night temperatures, increasing daily periods of darkness, decreasing daily periods of light, and, for some species, decreasing food supply.

The regularity in bird migration from year to year may be explained on the basis of these factors, particularly the length of day and night. It is a common observation that the arrival of species may be expected during the spring on or near the same date year after year. The daily increase in light and decrease in darkness during the spring and reverse during the autumn is a very regular phenomenon, and the timing of migration to these factors may account for the regularity of appearance and disappearance of a species in a region. The increase in temperature in the spring and decrease in the autumn is much less regular. The irregularities in the arrival and departure of species in any region may be explained by the superimposed influence of temperature upon the light factor. Differences in the availability of food from year to year is another contributing factor tending towards irregularity in bird migration, particularly in the autumn.

*Stimulus for migration*—Daily periods of light and darkness, temperature, and, to a lesser extent, availability of food regulate, according to the above discussion, the time of spring and autumn migration. This must be accomplished by some stimulus given to the bird at the proper time.

The work of Cahn (1925), Bergtold (1926), Rowan (1929), Heape (1931), and Schildmacher (1934) have recently emphasized the importance of a direct endocrinal stimulus for migration. These investigators believe that the actual stimulus for migration is due to endocrine secretion of the gonads, and that migration is as definitely a part of reproduction as is nest-building, egg-laying, and rearing of the young. Groebels (1928, 1932) postulates a more general physiological stimulus for migration in an unbalanced nutritional state of the bird in autumn and spring. This unbalanced nutritional state is occasioned by changing lengths of day and night, particularly in the autumn,



and by endocrine secretion, not only from the gonads, which is particularly important in the spring, but possibly also from other endocrine glands.

Certain endocrine glands, notably the thyroid, are known to be important in affecting the rate of metabolism in the body. There is some evidence also that an endocrine from the gonad may affect the body metabolism, in that castration of birds lowers by several percent. their rate of metabolism. (Mitchell, Card, and Haines 1927, Aude 1927). Possibly, the diminution in size of gonads in the fall may have a similar effect as castration, while the increase in size of the gonads in spring may raise the metabolism, but this has not been proved. The relative rate of metabolism of the bird is, in turn, vitally concerned in the bird's temperature resistance at different times of the year. Not only may the general body metabolism be regulated and modified by action of endocrines, but it is also effectively influenced by such environmental factors as temperature and length of day and night. Environmental factors, as length of day, also control, in large measure, the activity of the gonads and other endocrine organs themselves. Annual and daily rhythms in environmental factors are thus tied up with physiological rhythms in metabolism, endocrine action, and other physiological processes. Wachs (1926) emphasized the importance of annual physiological rhythms in stimulating birds to migrate, but he believed these rhythms to be independent of or only coincidentally related to environmental changes, and so minimized the all-essential point involved.

A composite picture of these rhythmic physiological changes may be tentatively formulated, although these changes are not yet well understood nor have they been actually measured and analyzed in full. Such a formulated picture applies only to birds breeding and wintering north of the equator. Those species that regularly winter close to or south of the equator present problems requiring special study, as they are in regions of nearly uniform daily periods of light and darkness throughout the year or are in regions where the periods of light and darkness are changing in just the reverse manner that they are in the northern hemisphere. A careful study of their physiological rhythms might show as close a correlation with environmental conditions as those now to be described, but undoubtedly certain points would need to be modified.

In the autumn, when air temperatures fall, the rate of metabolism and consequent heat production tend, on that account, to increase in order to maintain a constant body temperature. The nutritional state of the bird tends to become unbalanced from what it was in the summer, since more food is needed to allow for the potential increase in metabolism and also to supply the bird with more reserves in the body to carry them over the nights that are continually increasing in length. If the gonads exert any influence, it would be towards depressing the metabolism, thereby counteracting to some extent

the regulatory action induced by the drop in air temperature. This would tend to make the bird all the more sensitive to cold, by increasing the requirements for additional heat production as the air temperature continued to fall. Permanent resident species put on a thicker feather covering in the autumn, thereby compensating in large measure, if not entirely, for such requirement of increased metabolism and food consumption. In fact, the metabolism of birds in the autumn and winter after the molt is completed is less than it is in the summer at identical air temperatures. This allows, in the early autumn when air temperatures have not yet become greatly reduced and the energy requirements of nesting and molting are no longer needed, for a large percentage of the ingested food to become converted and stored as fat. Large food reserves in the body in the form of fat are necessary in late autumn and winter to tide the bird over the longer nights and during periods frequently lasting several days, when the air temperature falls to very low levels. During these later periods of extremity the metabolism is raised to a higher level in order to maintain the body temperature, the thyroid gland and perhaps other endocrine organs are more active to stimulate this increase in metabolism, and, ordinarily, sufficient fat and other food reserves in the body are available to supply this more rapid utilization. Species that migrate do not, apparently, respond physiologically in this matter to the extent as do those that remain as permanent residents. This is evidenced by the differences already noted between the house wren and mourning dove (migrant species) and the English sparrow and pigeon (permanent residents) in rate of metabolism, resistance to starvation, and endocrine activity (p. 338). As the food supply in the autumn becomes increasingly unavailable, this would necessarily add to the difficulty of some species in maintaining the proper metabolism and nutritional balance.

In the spring, when air temperatures rise and the nights become shorter, less energy and metabolism are required to maintain the temperature of the body. With the lengthening of the days, more food is consumed which allows for an increase in potential energy of the body that may now be expended for other activities than those concerned merely with self-preservation. As the gonads are at the same time stimulated by increasing daily periods of light to increase in size and activity, they apparently, stimulate, in turn, greater metabolism and activity of the bird concerning the duties of reproduction. However, as spring progresses, the air temperature becomes higher and higher during the middle of the day. This tends to depress the metabolism and eliminate the excess energy—all at the expense of normal activity, singing, and carrying on of the reproductive duties. To compensate for this unfavorable influence of rising daily maximum temperatures, the thyroid gland becomes less active and there is a continual decrease in the amount of plumage on the body. It is not known what effect the spring molt of certain

species may have here. In some species, this compensation is sufficient to allow them to remain as permanent residents throughout the breeding season. In other species, however, it appears to be insufficient, and the time finally comes when migration is compulsory, so that the bird may get into a more northern region where a better relation may be established between internal processes and environmental conditions, which will permit carrying on of the normal reproductive activities.

Changes in the body metabolism or the physiological state of the bird at different seasons of the year must, therefore, exert a powerful effect on behavior and activity. The actual conditioning influence determining migration appears to lie in this metabolic or physiological state of the organism. In order that this conditioning influence may exert any control over behavior, it must affect, in some way, the nervous system. Possibly the metabolic or physiological condition of the organism acts as a direct stimulus to the nervous system, or the condition may make itself felt indirectly by rendering the organism more sensitive to environmental stimuli received through the sense organs, or the nervous system may be influenced in both ways. Whatever the exact mechanism may be, the effective stimulus is controlled as to time and degree by the rhythmic physiological changes, interacting with such environmental factors as temperature, daily periods of light and darkness, and food supply.

*Nervous system involved*—The nervous system is necessarily involved in any such behavior of an animal as migration. Environmental control and physiological states can only regulate bird behavior through action of the nervous system. It is possible that a behavior or nerve pattern for migration has become established in different species of birds and needs only the proper stimulus for its release. Migration is actually controlled by the nervous system, and the nerve pattern may involve a definite set of neurons and synapses so that the resulting behavior tends to be uniform in all individuals. Some species appear to have this nerve pattern more rigidly established than do others, and, as a consequence, their migrations are more regular and definite. Since this nerve pattern, like other forms of behavior, does not function without the proper stimulus, the initiation of migration must be subject to stimuli that recur annually and must be subject to modification in order to meet changes in environmental conditions. Herrick (1910) has discussed in some detail the action of nerve patterns (instincts) and how the entire reproductive history of a bird, including migration, is guided by the overlapping of different nerve patterns. Wagner (1930) has found that, in caged birds, pronounced activity at night occurs only at the time of normal spring and autumn migration, and he has interpreted this as being a rhythmically recurring nervous unrest which would under normal conditions bring about migra-

tion. The question now arises as to how this nerve pattern may have become established with the consequent origin of the migratory behavior.

*Origin of migration*—Since migration in all likelihood originated before the last or Pleistocene ice age (Miller 1928, Mayr and Meise 1930), thousands of bird generations have doubtlessly been involved in its establishment. In pre-Pleistocene time, the evidence is uncertain as to the extent of the climatic zonation from the equator to the north pole, but probably some existed as did also differences in length of day and night at different latitudes. The amount of migration that then occurred would have been dependent on the degree of latitudinal differentiation. There can be no doubt, however, that with the advent of the ice age the climatic belts became accentuated and the development of the migratory behavior hastened. Temperature then varied markedly between different parts of the country and at different seasons of the year. The birds were adjusted in their physiology and behavior to certain fairly constant environmental conditions and so sought to maintain themselves in these conditions when climatic factors began to vary and approach their limits of tolerance.

Individuals or species may have first sought relief, when the climatic environment became unfavorable, by wandering in all directions, but, after an indefinite number of trials and errors, they or their descendants would learn that relief lay in one direction rather than another. Young birds would be taught where and when to migrate by following their parents or other adult birds of the same species or may even have followed birds of other species already moving in a definite direction. Later, as experiences accumulated, rising temperatures in the south during the spring would direct the birds in their wanderings away from regions where temperatures daily became warmer, into regions northward where they were more favorable. In the autumn the reverse would be true, because falling temperatures together with other factors becoming unfavorable would cause the birds to move south rather than north. The distance of migration would at first not be great because variations in climate would not be great, but later they would become more extensive as changes in climate became more extreme.

At first, the migration would not be well regulated. The stimulation for wandering may have been weak and may have covered a period of weeks. The birds would then have moved out of a region gradually becoming unfavorable any time during this period of low stimulation. However, the region to which they moved would not have favorable conditions constantly. As one region was gradually becoming unfavorable, the other would be equally as gradually becoming favorable. Too early migration out of one region would precipitate the species too soon in the other. The most favorable period would be discovered, however, after several trials by the same individual or by following generations. Knowledge gained by one gen-



eration would be transmitted by example to the next. Those individuals that wandered astray or made too bad mistakes as to time of migration would in most cases be killed. The behavior of the birds would gradually become adjusted so that the most appropriate time to migrate would be assumed in order to take best advantage of average conditions in both the summer and winter ranges. This adjustment would become more definite and exact as the climatic variations became more extreme. Undoubtedly, if climatic conditions should return to what they were before the advent of the ice sheet and more uniform climatic conditions again prevailed from the equator to the Arctic, migration would lose much of its regularity and many species would become permanently resident in the different regions (Grinnell 1931).

The extent of the spring and autumn migration was probably determined in large part by physiological limits of tolerance and environmental conditions. Most birds now terminate their migration in regions that appear well suited for their reproduction or for their survival during the season. In many species, the extent of migration is modified from year to year by environmental conditions. For instance, individuals of certain species remain in northern Ohio during warm winters but migrate further south during cold winters. In contrast to this, other species appear always to migrate further than is necessary, some as far as South America. It may be that the physiological reactions of these birds to environmental conditions are more complicated, or their extended migrations may be due to a difference between ancestral and present day conditions to which the birds have not responded.

Under the guiding influences of interacting environments and physiological conditions, such as are above described, definite nerve patterns could have become established in the nervous system of the bird. The forming of nerve patterns would establish the migratory behavior more securely and tend to stereotype the responses of the bird. Since the nerve pattern, according to this interpretation, is a definite system of neurons and synapses, it is fundamentally of a morphological character. It would be subject to evolution like any other morphological character and be exposed to modification by mutations of the chromosomes and by processes involved in development. A discussion of the genetical factors involved in the evolution of a nerve pattern is beyond the scope of this paper. Nice (1933) has recently contributed to the genetics of migration. Mention needs only to be made of the importance in this evolution of the habit that many species of birds have of going in groups. Bird-banding operations, carried on now for several years, indicate that, with several species of sparrows and warblers, groups of individuals are formed that migrate together, winter together, and breed in the same general region (Baldwin 1921, Whittle 1923, 1926, Fletcher and Whittle 1924, Higgins 1926). Inexperienced birds in these species may be shown the route of migration and appropriate breeding and wintering areas

by older members of the group. Nolte's paper (1927) is of interest in this regard, as is also that of Brewster (1886). Experience and knowledge gained by one generation could be handed on within the group to the succeeding generation as a sort of social inheritance. In this way, time would be available for the nerve pattern itself to become fully established or appropriately modified.

#### FACTORS CONTROLLING ABUNDANCE

*Regionally*—Around the periphery of the species' breeding and wintering areas, the eastern house wren decreases in abundance before it disappears. This is what would be expected as environmental conditions approach closer and closer to the limits of tolerance. Only the most hardy individuals can meet these conditions, and so the number of individuals of the species represented in the area is small. An exception to this general statement must be made where the limits of the bird's distribution is controlled by a physiographic feature. In such cases, there is no diminution in numbers of the species around that side of the periphery. The factors that are effective in decreasing the abundance of the species towards the limits of its distribution are the same that are effective in determining those limits themselves. Local variations in the abundance of the bird throughout its area may be due to variations in these same factors and also in availability of nesting sites and nesting territories.

*Yearly*—The numbers of many and perhaps most species of animals fluctuate from year to year. This is due, in part, to variations in environmental conditions. In order to analyze the effect of these external factors in the case of the house wren, the two most important items involved, amount of reproduction and survival over winter, were studied separately.

The reproductive activity of individual house wrens varies inversely with the number of breeding pairs present in the area from year to year. The relative amount of reproduction is correlated positively with average night temperature and inversely with velocity of wind and number of enemies.

The relative rate of survival over winter is correlated positively with variations in average night temperature during the winter and spring, positively with relative humidity during the winter, positively with the actual amount of sunshine daily during the autumn and winter, positively with precipitation during the spring, and inversely with the velocity of wind during the winter and spring.

#### FACTORS CONTROLLING RÔLE OF ANIMALS IN ECOLOGICAL COMMUNITIES

Without entering into a lengthy discussion, the significance of this study to the consideration of ecological communities, mentioned in the Introduction, may be briefly summarized. Contrary to the prevalent idea among some

ecologists, plants are not necessarily more responsive than animals to climatic influences. Animals, particularly birds, do not simply exist in the conditions established by plants and are not exclusively controlled by them alone; rather, animals are also sensitive and responsive to climatic factors and their distribution, occurrence, abundance, and behavior are in large measure controlled by these factors. The relation of animals in the biotic community is determined in part by interdependence with plants, but the community of animals as well as of plants is an expression and a result of particular and definite climatic and environmental conditions.

## XI. CONCLUSIONS

1. The eastern house wren, *Troglodytes a. aedon* Vieillot (footnote, p. 301), coincides in its distribution during the season of reproduction with the *Acer-Fagus* (maple-beech) Association of the *Quercus-Fagus* (oak-beech) Formation. The species occurs most commonly as a member of a seasonal societies in subclimax or seral stages of ecological successions (seres) in the area and may be taken as representative in its behavior of a portion of the passerine avi-fauna of these ecological communities.

2. There are zones of physiological discomfort and limits of physiological tolerance to excessive increases or decreases in environmental factors, such as temperature (p. 340), which are important in controlling the behavior, distribution, migration, and abundance of birds. The exact limits of physiological tolerance varies with the species. From experimental studies, the critical factor in the effect of low temperature is shown to be the average temperature at night, but this is important only in conjunction with the number of hours of darkness during which the bird must remain without food. The critical factor in the effect of high temperature is the mean daily maximum temperature which is ordinarily attained in the afternoon. Other unfavorable environmental factors are short periods of daylight, too low and too high intensity of solar radiation, lack of available food, too intense biotic competition, lack of nesting territory and nesting sites, and unfavorable physiographic features.

3. Much of the behavior of birds is a response to the interaction of physiological potentialities and environmental conditions and is adjusted to maintain the best possible relation between the two for the existence of the individual and the reproduction of the species.

4. The northward distribution of the eastern house wren during the breeding season appears to be limited primarily by low night temperatures for which the shortening of the daily periods of darkness does not entirely compensate. The southward distribution appears to be primarily controlled by high daily maximum temperatures and competition with the Bewick wren, *Thryomanes b. bewicki* (Audubon). The eastward limit of the breeding

range is determined by the Atlantic Ocean, while a decrease in relative humidity and precipitation may be directly or indirectly concerned in the westward transition from the eastern to the western subspecies of the house wren. Other factors are of uncertain or secondary importance.

5. The wintering area of the eastern house wren is limited on the north by low night temperatures combined with long daily periods of darkness, short daylight periods, low intensity of solar radiation, snow, and lack of available food. On the east, the wintering area is limited by the Atlantic Ocean, on the south by the Gulf of Mexico, and on the west by much the same conditions, perhaps, that are effective during the breeding season.

6. The southward migration of the eastern house wren in the autumn is necessary for the continued existence of the species, while the northward migration in the spring avoids unfavorable breeding and existing conditions in the south. By migrating south in the autumn and north in the spring, the bird maintains itself in a more nearly uniform and favorable environment throughout the year. The regulation of migration as to time is controlled in the spring by rising daily maximum and night temperatures and changing relative proportions daily of light and darkness. In the autumn, decreasing temperatures particularly at night, longer nights and shorter days, and, for some species, decreasing food supply are most important. The conditioning factor that may act directly or indirectly as a stimulus for initiating migration is an excessive change in the metabolic or physiological state of the body. Changes in physiological state are induced by and correlated with changes in environmental conditions, both directly and through the intervention of the endocrine system. The nervous system is involved for responding to this stimulus and for organizing the resultant migratory behavior of the bird. Inherited nerve or behavior patterns, aided by social inheritance, are probably fundamental in maintaining the same migratory behavior from generation to generation and in determining the direction, time, and extent of the migration. The origin of migration among birds is traced to pre-Pleistocene time and the establishment of seasonally fluctuating environmental conditions.

7. Variations in regional abundance of a species is determined in large measure by variations in environmental conditions, principally those of temperature, solar radiation, and competition with other species. Local abundance depends largely on these same factors and on availability of food, nesting sites and nesting territories. Variations in the abundance of a species in the same locality during consecutive years is dependent upon the number of birds breeding during the previous year, the amount of reproduction, and the survival over winter. The reproductive activities of individual birds varies from year to year inversely to fluctuations in numbers of breeding pairs of that species in the area. The relative amount of reproduction is correlated positively with average night temperature and inversely with velocity of wind



and number of enemies. Variations in rate of survival over winter are correlated positively with variations in average night temperature, relative humidity, solar radiation, and precipitation and inversely with velocity of wind. These factors vary in their relative importance during autumn, winter, and spring.

8. The general conclusion of this study is that climate is a factor of major importance in controlling the distribution, migration, abundance, and behavior responses of the smaller passerine birds in the ecological biotic communities of eastern North America.

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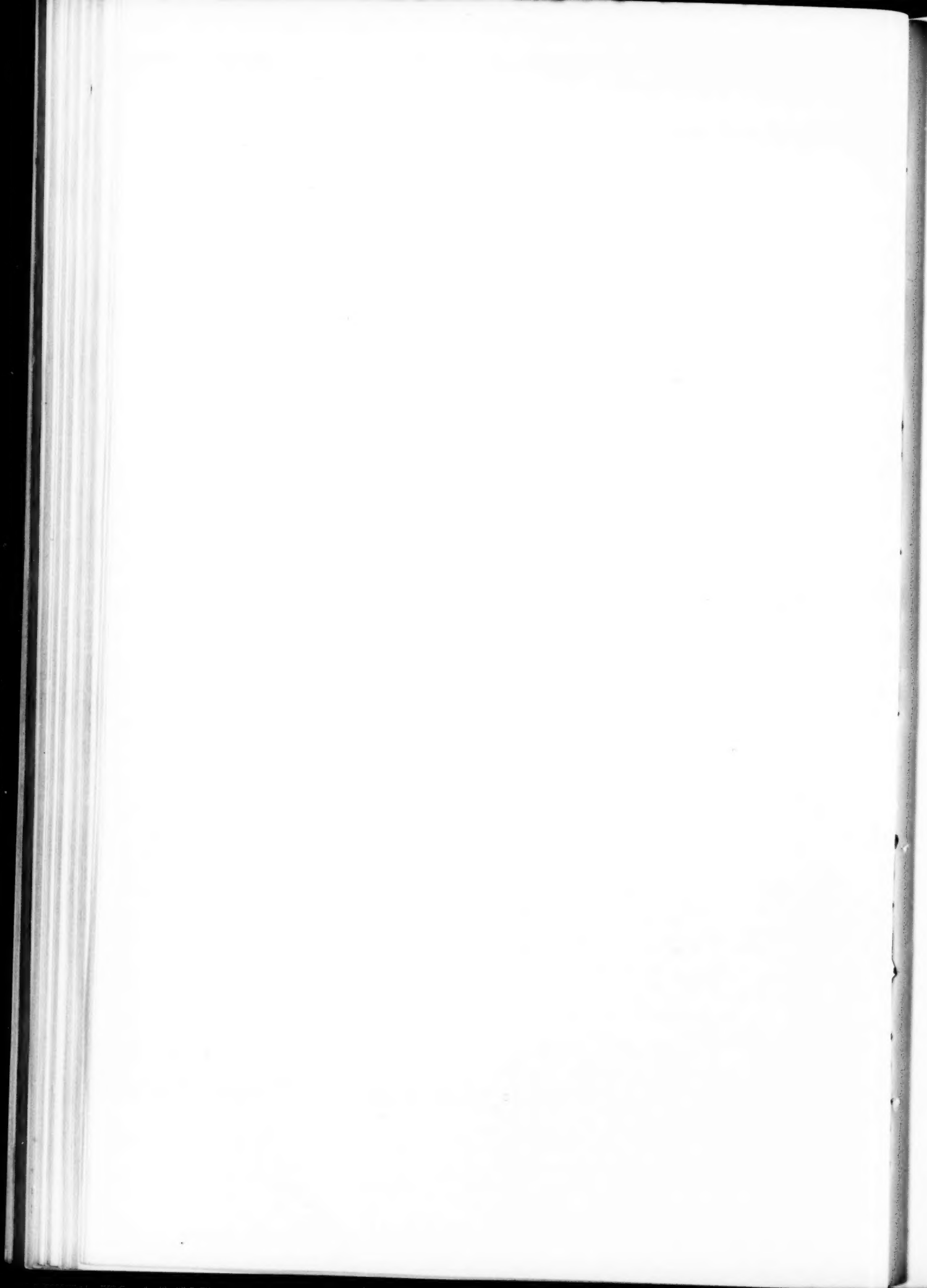
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